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PROCEEDINGS OF THE NINTH NORTH AMERICAN PRAIRIE CONFERENCE

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NORTH AMERICAN PRAIRIE CONFERENCES

The Ninth North American Prairie Conference was the most recent of a series of biennial meetings begun in 1968. The first conference was held 14-15 September at Knox College, Galesburg, Illinois, the second 18-20 September at the University of Wisconsin, Madison, the third 22-23 September 1972 at Kansas State University, Manhattan, and the fourth 19-22 August at the University of North Dakota, Grand Forks. Through the fifth, held 22-24 August 1976 at Iowa State University-Ames, the meetings were referred to as the Midwest Prairie Conference.

Reflecting the broadening interest in native grassland and savanna, later meetings have been termed the North American Prairie Conference. The sixth was held 12-17 August 1978 at Ohio State University, Columbus, the seventh 4-6 August 1980 at Southwest Missouri State University, Springfield, and the eighth 1-4 August 1982 at Western Michigan University, Kalamazoo.

Below are listed the published proceedings reporting each conference.

Schramm, Peter, Editor. 1970. *Proceedings of a Symposium on Prairie and Prairie Restoration*. Knox College BIological Field Station Special Publication No. 3. 66 pp. $5.50 postpaid. Contact Schramm, Knox College, Galesburg, Illinois 61401 and make check payable to Peter Schramm.

Zimmerman, James H., Editor. 1972. *Procedings of the Second Midwest Prairie Conference*. 242 pp. Published by the editor. 2114 Van Hise Ave., Madison, Wisconsin 53705. $8.50 postpaid. Make check payable to James H. Zimmerman at above address.

Hulbert, Lloyd C., Editor. 1973. *Third Midwest Prairie Conference Proceedings*. Division of Biology, Kansas State University, Manhattan, Kansas 66506. 91 pp. $6.00 postpaid. Make check payable to Division of Biology.

Wali, Mohan K., Editor. 1975. *Prairie: A Multiple View*. The University of North Dakota Press, Grand Forks, North Dakota 58202. 433 pp. $10.00 + postage. Make check payable to University of North Dakota Press. (Pemble, Richard H., Ronald L. Stuckey, and Lynn E. Elfner. 1975. Native Grassland Ecosystems East of the Rocky Mountains in North America, a Preliminary Bibliography. A Supplement to Wali [1975]. Ca. 7000 references. 466 pp. $7.00 + postage. Make check payable to University of North Dakota Press.)

Glenn-Lewin, David C., and Roger Q. Landers, Jr., Editors. 1978. *Fifth Midwest Prairie Proceedings*. Extension Courses and Conferences, 102 Scheman Continuing Education Building, Iowa State University, Ames, Iowa 50011. 230 pp. $3.50 postpaid. Make check payable to Iowa State University.

Stuckey, Ronald L., and Karen J. Reese, Editors. 1981 [1982]. *The Prairie Peninsula - in the 'Shadow' of Transeau: Proceedings of the Sixth North American Prairie Conference*. Ohio Biological Survey Biological Notes No. 15. 278 pp. Ohio Biological Survey, 484 W. 12th Ave., Columbus, Ohio 43210. $12.50 + postage. Make checks payable to Ohio Biological Survey.

Kucera, Clair L., Editor. 1983. *Proceedings of the Seventh North American Prairie Conference*. Southwest Missouri State University, Springfield, Missouri 65802. $18.00 postpaid. Order from Department of Biology and make check payable to Southwest Missouri State University.

Brewer, Richard, Editor. 1983. *Proceedings of the Eighth North American Prairie Conference*. Department of Biology, Western Michigan University, Kalamazoo, Michigan 49008. $28.00 postpaid. Make check payable to Western Michigan University.

Clambey, Gary K. and Richard H. Pemble, Editors. 1986. *The Prairie - Past, Present and Future: Proceedings of the Ninth North American Prairie Conference*. Tri-College University, 306 Ceres Hall, North Dakota State University, Fargo, North Dakota 58105. $20.00 postpaid. Make check payable to Tri-College University.

THE PRAIRIE: PAST, PRESENT AND FUTURE

PROCEEDINGS OF THE NINTH NORTH AMERICAN PRAIRIE CONFERENCE

Held July 29 to August 1, 1984, Moorhead, Minnesota

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PREFACE

"The vast ocean of level prairie...must be seen in its extraordinary aspects..."

Such were the words of one visitor recording his impressions of the valley of the Red River of the North in 1857.

Immense herds of bison, elk, grizzly bear, and wolves...all these and more were part of the Red River Valley region prior to European settlement in the late 1800s. While these animals have vanished, the Red River Basin of Minnesota, North Dakota, South Dakota, and Manitoba still provides excellent opportunities to experience, firsthand, the prairie past.

The southern part of the Red River Basin was selected as the site for the Ninth North American Prairie Conference. The theme chosen for the conference was "The Prairie: Past, Present, and Future." This theme reflected popular topics of previous conferences such as prairie ecology, restoration, interpretation, and preservation, and it also suggested a new topic for consideration—the prairie past. The prairie past includes not only the natural history of the prairies but also the role of pre-European people in prairie ecosystems.

Between July 29 and August 1, 1984 more than 550 prairie enthusiasts gathered on the campus of Moorhead State University for the Ninth Prairie Conference. The conference was hosted by the Tri-College University Center for Environmental Studies and its three member schools—Concordia College and Moorhead State University in Moorhead, Minnesota, and North Dakota State University in Fargo, North Dakota. The conference registrants, representing 26 states and three Canadian provinces, came with interests ranging from bison to Plains Indians to wildflowers and grassland fires. Keynote addresses by nationally known prairie researchers, field trips to surrounding grassland sites, workshops, displays, an exhibit of photographs on American bison, a prairie color slide contest, a landscape design awards competition featuring prairie motifs, and more than 160 contributed papers were featured in the four-day conference.

Abstracts of all the contributed papers were published in an abstract booklet which was available to conference registrants. A few of these booklets are still available at a cost of $3.00 each postpaid from Dr. R. H. Pemble, Department of Biology, Moorhead State University, Moorhead, MN 56560. Checks should be made payable to the TCU-CES.

This volume, the *Proceedings of the Ninth North American Prairie Conference*, contains in manuscript form 60 of the papers which were presented at the conference. Each of the manuscripts has been reviewed by one or more persons outside the editorial staff. Reviewers are listed on page *vi*. We are most grateful for their careful reviews, constructive criticism, and prompt responses. We are also grateful to the authors who provided prompt, responsive revisions, even when such revisions required substantial modifications of the original manuscript. A special acknowledgement must be given to Jacqui Paulson and Margot Peterka for their extraordinary efforts in bringing this volume through the final stages of publication. Jacqui served not only as a typist but as a most capable proofreader. Margot Peterka's efforts were definitely beyond the call of duty. Margot, who handled the design and production of the *Proceedings* took the responsibility for numerous details, all of which contributed to the quality of this volume. We thank them both.

The arrangement of papers in the *Proceedings* does not correspond exactly to the organization of the sessions for contributed papers at the conference. We have consolidated the original seventeen conference sessions or sub-sessions to nine sections in this volume. The papers which are included represent the full spectrum of topics which were addressed by conference presenters. The *Proceedings* offer a wealth of information about prairie ecosystems. One need only scan the Table of Contents to appreciate the diversity of expertise represented at the conference.

Not only do the Prairie Conferences provide a forum for sharing ideas, they also provide an opportunity to establish new and renew old friendships. A significant number of conference registrants have been in attendance at most of the Prairie Conferences held over the past eighteen years. They have become our friends and we look for their faces at each conference, saddened when they are not to be seen. One such individual who was with us in Moorhead and at most of the previous conferences will be greatly missed in the future.

Dr. Lloyd Hulbert, a long-time faculty member at Kansas State University and nationally recognized prairie expert and enthusiast, died on May 23, 1986 after a lengthy battle with cancer. Lloyd chaired the Third Prairie Conference hosted by Kansas State University in 1972, but he was best known to most of us for his research on the effects of fire in tallgrass prairie ecosystems and his role in establishing the 8,616-acre Konza Prairie. Lloyd dedicated his life, both professionally and personally, to furthering our understanding of how we interrelate with each other and all of life. It is the opportunity to interact with individuals like Lloyd Hulbert which makes the North American Prairie Conference truly worthwhile.

Gary K. Clambey
Richard H. Pemble
October 1986

Part 1. PRE-EUROPEAN PEOPLE ON THE PRAIRIES

PLANTS AND PEOPLE: PAST ETHNOBOTANY OF THE NORTHEASTERN PRAIRIE

C. Thomas Shay
Anthropology Department, University of Manitoba, Winnipeg R3T 2N2

Abstract. Ethnobotany is the study of how humans relate to plants. This paper explores the ethnobotany of native hunters and gatherers, native farmers and 19th century European fur traders in the northeastern prairie. While the region's long winters, low rainfall and limited forests challenge its inhabitants, it is endowed with a variety of resources including more than 300 useful plant species. Botanical remains from prehistoric sites reveal that several types of berries and weed seeds were collected by early hunters. These wild species continued to be used after aboriginal agriculture was introduced 1,000 years ago. Key foods of historic native tribes included *Acer negundo* sap, *Psoralea esculenta* roots and *Prunus virginiana* berries. Agricultural crops included *Zea mays*, *Cucurbita* spp., *Phaseolus vulgaris*, *Helianthus annuus* and *Nicotiana rustica*. Native tribes used local forests for fuel and construction but had relatively little impact on them. But because of their greater demand, fur traders depleted local forests and were obliged to import wood from a distance. Through such depletion, land clearance and the introduction of Old World species, the Europeans had a much greater impact on the landscape than either native hunters and gatherers or native farmers. European exploitative attitudes contrast with the spiritual bonds that tied native people to the land.

INTRODUCTION

The prairie is more than wind-swept soil, beckoning flowers and waving grass. It is a state of mind - shaped by the way people relate to its plants, animals and other resources.

The bond that developed between native people and plants is illustrated in the legend of Wapee (Brown 1970). The legend tells us that, to enter adulthood, Wapee had to spend four days and nights atop a lonely hill until he had a vision. The first night no vision came. The next day the rising sun shone on a beautiful flower and its open petals nodded as if to welcome him. Wapee no longer felt alone. When night returned, he curled his body around the plant to protect it from the icy winds. Three times he did this and three times when the morning star appeared, he was rewarded with visions foretelling great things. When Wapee rose to leave, he said to the plant, "You have counselled me well. What three wishes would you have me ask of the Great Spirit?" The flower replied, "Pray that I may have the purple blue of the distant mountains in my petals, a small golden sun to hold close to my heart and a furry coat to face the cold winds of spring." The Great Spirit was so pleased with Wapee's thoughtfulness that he granted his wishes. To this day, the prairie crocus has purple petals, a yellow center and a velvety hairy coat. This spiritual bond with plants was typical of native North Americans (Hughes 1983).

Ethnobotany focuses upon the way in which human societies relate to plant life. As a hybrid of anthropology and botany (Fig. 1), it embraces both human values and plant biology. Both play a part in how plants are selected and used. Aesthetic preferences and values heavily influence the choice of religious and social symbols such as our Easter lilies and carnation corsages, but abundance and heat yield most often guide the choice of firewood (Ford 1979). Human values and natural properties share about equally in the selection of food (Ford 1979, Krondl and Boxen 1975).

In a broader sense, a society's attitudes toward nature affect its exploitation of the environment. Exploitation in turn alters the society's culture and the environment. For example, the adoption of wild rice gathering among the prehistoric people of the Great Lakes provided a new protein-rich food which allowed more people to be supported. It also influenced technology and the seasonal movements of the people (Rajnovich 1984). Domestication of the world's major food crops over the past 10,000 years has not only transformed the food supply, it has significantly altered human nutrition, population numbers, settlement patterns, social life, religion and values (Harlan 1975). Exploitation may leave deep imprints on the environment. Plant domestication, the spread of exotic species, fire, land clearance and selective harvesting are among the changes that have profoundly altered the face of the earth (Thomas 1956).

The following pages focus upon the northeastern prairie and how people with several cultural traditions related to its plant life. These relationships are explored for native hunters and gatherers, native farmers and 19th century fur traders. The aims are to: 1) examine the role of plants among these peoples, 2) illustrate their attitudes towards plants and the natural landscape, and 3) note the influence of each lifestyle on prairie vegetation and plant distributions.

THE NORTHEASTERN PRAIRIE ENVIRONMENT

The northeastern prairie (Fig. 2) includes the tall and mixed grasslands that stretch from western Minnesota to western North Dakota and from southern Manitoba and Saskatchewan to South Dakota (Weaver 1954, Weaver and Albertson 1956, Whitman and Wali 1975). Aspen parkland and oak savanna mark the transition from the prairie to the eastern and northern forest (Bird 1961, McAndrews 1966). South and west of this partially wooded fringe, forests are confined to stream valleys, around lakes and on steep escarpments (Küchler 1964, Wells 1970, Burgess et al. 1973, Wali et al. 1980).

With its long cold winters, low rainfall and periodic drought (Borchert 1950), the region challenges its inhabitants. Nevertheless, it contains more than 1,500 flowering plants (estimate based upon

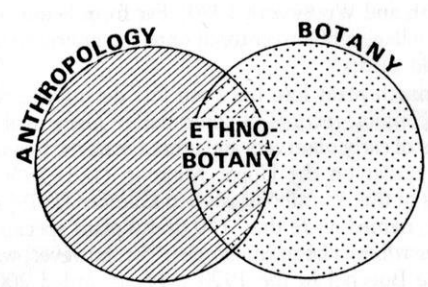

FIG. 1. Ethnobotany, a meeting ground of anthropology and botany.

Rogers 1980b and Barkley 1977). About 300 of them can be eaten; several hundred more can be used for other purposes - as medicines, religious symbols, ornaments, toys, construction materials and fuel.

PREHISTORIC PLANT USES

The uses of certain plants can be traced into prehistory, thanks to the emerging pursuit of paleoethnobotany, the study of ancient plant uses.

Nomadic hunters and gatherers made the northeastern prairie their home for more than 10,000 years (Wedel 1961), although past plant uses are described here for sites spanning only the past 4,000 years. About 1,000 years ago, native farmers settled along the Missouri and other major river valleys (Lehmer 1971).

Insights into the ethnobotany of these prehistoric peoples come from charred seeds and wood charcoal from several excavated sites in the northeastern prairie (Fig. 3). A comparison of plant remains from two hunting and gathering camps with those from three agricultural villages (Table 1) reveals several similarities and differences. The striking similarity is that some of the same berry and weed seeds are found in both types of sites, suggesting that prehistoric villagers did not abandon wild plant collecting when they took up farming. The agricultural villages also contain the remains of the cultivated crops - corn (*Zea mays*), beans (*Phaseolus vulgaris*), squash (*Cucurbita pepo*), sunflower (*Helianthus annus*), and tobacco (*Nicotiana rustica*).

Wood charcoal from the remains of cooking and heating fires offers further insight into local plant use. Charcoal from three prehistoric hunting and gathering sites in North Dakota and southern Manitoba (Table 2) roughly reflects the present local vegetation around each site. Some species were apparently favored: the charcoal of green ash (*Fraxinus pennsylvanica* var *lanceolata*) predominates at two of the sites. Plant nomenclature for indigenous species follows Stevens (1963) although some Canadian common names from Scoggan (1957) have been added.

Green ash charcoal has also been found at several agricultural villages along the Missouri River near Bismarck, including Shermer (Sperry 1968) and Cross Ranch (Calabrese 1972). Other charred woods from Shermer were oak (*Quercus*), pine (*Pinus*), juniper (*Juniperus*), and cottonwood (*Populus*) and/or willow (*Salix*). House posts at Cross Ranch were made of green ash, cottonwood, juniper, willow, elm (*Ulmus*), wild plum (*Prunus*) and hackberry (*Celtis occidentalis*). The use of such a variety of woods may reflect the villagers' demands for fuel and building materials.

ETHNOBOTANY OF HISTORIC NATIVE TRIBES

Native cultures in the northeastern prairie gradually became transformed under the influence of European contact that began in the 18th century. Until about the middle of the 19th century, the region remained the home of nomadic hunters and gatherers and sedentary agricultural peoples. These included the bison-hunting Assiniboin, Plains Cree, Plains Ojibwa and Western Dakota while along the Missouri River were the farming villages of the Mandan, Hidatsa and Arikara (Lowie 1954, Denig 1961, Howard 1965, Ewers 1968). The Eastern Dakota in southern Minnesota also farmed (Woolworth and Woolworth 1980). Far from being completely sedentary, villagers often ventured onto the prairie to hunt and to gather wild plants.

Although much plant lore has been lost during the centuries of European contact, records of some native plant uses survive in the writings of early observers and ethnobotanists. Edwin Denig (1930), a fur trader on the Upper Missouri (1833-1856), listed 20 plant foods of the Assiniboin; Melvin Gilmore (1919) an early ethnobotanist, named more than 150 useful plant species for the Missouri River tribes. The most complete list, however, was made by Fr. Eugene Buechel in the 1920's. He recorded 200 useful species among the Western Dakota of the Rosebud area in southern South Dakota (Rogers 1980a).

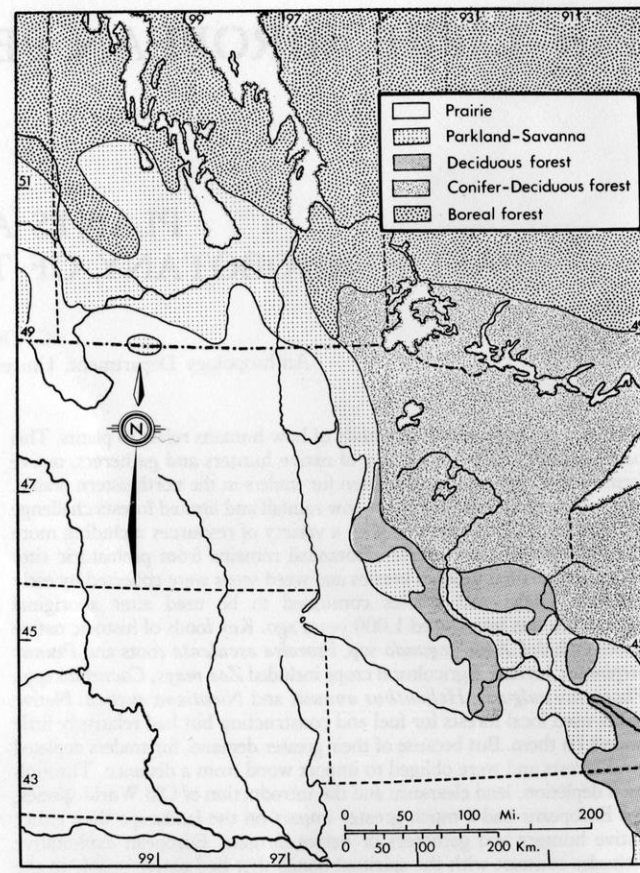

FIG. 2. The northeastern prairie. Vegetation boundaries for the U.S.A. after Küchler (1964) and for Canada, Rowe (1972).

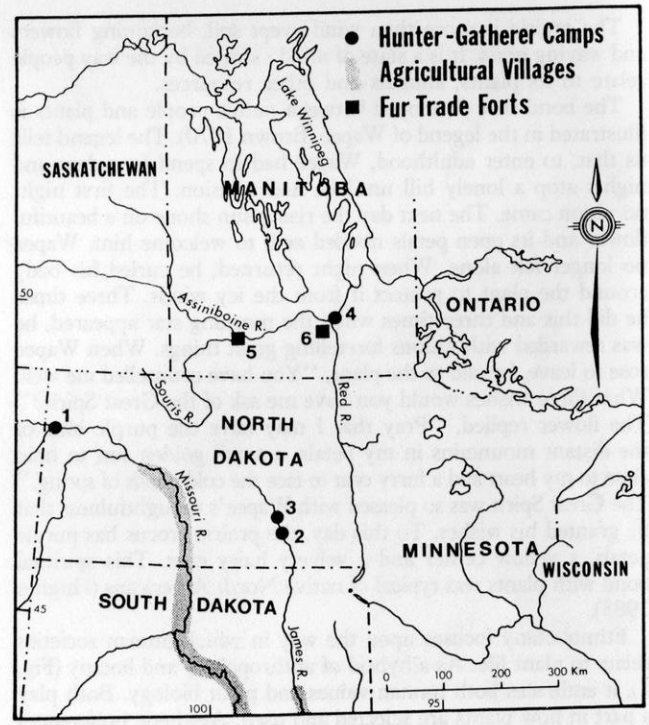

FIG. 3. Selected archaeological sites in the northeastern prairie where plant remains have been analyzed. 1 - Mondrian Tree, 2 - Naze, 3 - Jamestown, 4 - McAuley, 5 - Souris Mouth post, 6 - Upper Fort Garry. Prehistoric and historic agricultural villages were located in the shaded portions of the Missouri and James river valleys as well as in southern Minnesota. See Tables 1-3 and text for the locations of the sites not shown.

TABLE 1. Presence (x) of selected seed types from archaeological sites in the northeastern prairie.

	Hunting & Gathering Camps		Farming Villages		
	Mondrian[1] Tree	Naze[2]	White Buffalo Robe[3]	Mitchell[4]	Chan-ya-Na5
CULTIGENS					
Maize (Zea mays)			x	x	x
Beans (Phaseolus vulgaris)			x	x	x
Squash (Cucurbita pepo)			x	x	x
Sunflower (Helianthus annuus)			x	x	x
Tobacco (Nicotiana rustica)			x	x	x
BERRIES & FLESHY FRUITS					
Wild plum/cherry (Prunus)	x	x	x	x	x
Wild rose (Rosa)	x	x	x	x	
Buffalo berry (Shepherdia argentea)			x		
Wolfberry (Symphoricarpos)	x	x			
Wild grape (Vitis)	x		x		x
Sumac (Rhus)	x			x	x
WEED SEEDS					
Goosefoot (Chenopodium)	x		x	x	x
Pigweed (Amaranthus)				x	x
Knotweed (Polygonum)	x			x	x
Dock (Rumex)			x	x	
Marsh elder (Iva)	x			x	

[1] On terrace of Missouri River, western North Dakota, cultural zones 4-6, ca. 880-2180 B.C.; 31 waterscreen and flotation samples with about 300 seeds (Shay, Hansen and Gennett 1983).

[2] On terrace of James River, southeastern North Dakota, south of Jamestown, ca. O A.D. to historic; three waterscreen samples totalling 27 seeds (Good et al. 1977).

[3] On upland adjacent to Missouri River, central North Dakota, ca. A.D. 1300-1845; 288 waterscreen samples with several thousand seeds (Nickell and Jones 1980).

[4] On upland above Firesteel Creek near Mitchell in southeastern South Dakota, ca. A.D. 985-1125; 77 flotation samples with about 1500 seeds (Benn 1974).

[5] On upland flanked by steep ravines, Buena Vista County, northwestern Iowa, ca. A.D. 995-1215; flotation samples totalling about 3500 seeds (Wegner 1979).

TABLE 2. Charcoal found at prehistoric hunting and gathering sites in the northeastern prairie.

	Western North Dakota Mondrian[1]		Eastern North Dakota Jamestown[2]		Southern Manitoba McAuley[3]	
Tree type	Local vegetation	Charcoal	Local vegetation	Charcoal	Local vegetation	Charcoal
Elm (Ulmus)	x	x	x	x	x	x
Ash (Fraxinus)	x	x	x	x	x	x
Box-elder/Maple (Acer)	x	x	x	x	x	x
Poplar-Cottonwood (Populus)	x				x	
Willow (Salix)	x	x[4]			x	
Basswood (Tilia)			x			
Oak (Quercus)			x	x		

[1] On terrace of Missouri River, cultural zones 4-6, ca. 880-2180 B.C., n = 36 charcoal pieces (Shay, Hansen and Gensett 1983).

[2] On terrace of James River in Jamestown. Two mounds (32SN22), components I-IV, ca. A.D. 200-1700; (Shay and Zwiazek nd., Shortland-Coles nd.) n = 46 charcoal pieces.

[3] On terrace of Red River, East Kildonan in Winnipeg ca. A.D. 1000, n = 24 charcoal pieces (Shay, unpublished).

[4] Poplar and/or willow.

Not all species were equally important. A few were staples, others were needed only for certain ceremonies or unusual ailments and some were too rare to be anything but occasional treats. Whatever its use, a plant was always gathered with care to ensure its continued supply (Hughes 1983). When and how much to collect was based upon familiarity with plant life cycles and reproductive requirements.

People also learned from plants. Walking Buffalo, a member of the Stoney (Assiniboin) tribe said:

> Did you know that trees talk? Well they do. They talk to each other other and they'll talk to you if you listen... I have learned a lot from trees: sometimes about the weather, sometimes about animals, sometimes about the Great Spirit. (In Hughes 1983:49).

Plants pervaded all aspects of native life and served native needs throughout the year. A prairie year is marked by sharp contrasts from one season to another, each with its typical subsistence pursuits. These pursuits, largely geared to hunting or agriculture, had an annual rhythm in which plant-gathering played a role. In late winter, nomadic hunting groups could be found in sheltered woodlands. The reason was simple: when game was scarce and provisions low, the inner bark of cottonwood (*Populus deltoides*) could ward off famine. In groves of box- elder/Manitoba maple (*Acer negundo*) sap was tapped and boiled down to maple sugar (MacLeod 1955). As sap dripped into birch bark pails, children scurried to find enough wood for the boiling cauldrons to prepare their sugary treat.

With spring came young shoots and leaves of such species as goosefoot (*Chenopodium* spp.) and dock (*Rumex* spp.) which were eaten raw or cooked. As ducks and geese returned, prairie marshes and potholes attracted nomads for plant gathering as well as hunting. Succulent shoots of bulrush (*Scirpus validus*) and cat-tail (*Typha latifolia*) could be harvested in quantity. Like many other species, cat-tails served many purposes. The starchy roots and rhizomes dug in the fall or early spring were dried and pounded into meal, young flower spikes were boiled and eaten, and the pollen from mature spikes was used for flour. Cat- tail leaves were woven into mats and baskets, and the fluffy down of the ripe seed heads was used for dressing wounds and padding diapers (Gilmore 1919, Rogers 1980b).

As the nomads journeyed across the prairies throughout the spring and summer, useful plants were always at hand. One important food was the prairie turnip (*Psoralea esculenta*) (Reid 1977, Kaye and Moodie 1978, Wedel 1978). Imagine small children combing through the grass until they discovered the turnip's silvery leaves. Hearing their children's joyful squeals, mothers would arrive with their digging sticks, and soon, plump tap roots would go into their baskets. The fibrous pea-flavored roots are as nutritious as domesticated potatoes and will keep for months either dried whole or pounded into flour.

Although strawberries (*Fragaria* spp.) were a tasty treat in early summer, it was not until July and August that wild fruits could be gathered in quantity (Gilmore 1919, Rogers 1980a, 1980b). Woodland margins and thickets became hives of activity as women and children harvested the ripe fruit. An animal hide would be spread on the ground and the berry bushes beaten until the fruit dislodged. Juneberry/Saskatoon (*Amelanchier* spp.), raspberry (*Rubus* spp.) and sometimes the common but bland wolfberry (*Symphoricarpos occidentalis*) were sought. The fruits of rose (*Rosa* spp.) and hawthorn (*Crataegus* spp.) were also gathered but the premier fruit was chokecherry (*Prunus virginiana*). The Western Dakota named the month of July after the chokecherry which ripened at that time. After sun drying, the berries were pounded and mixed with buffalo meat and fat to make pemmican - a staple food for natives and European traders.

Common ailments were treated with medicinal plants found in virtually any patch of prairie (Gilmore 1919, Rogers 1980a, 1980b). These included purple cone-flower (*Echinacea angustifolia*), wild bergamot (*Monarda fistulosa*), prairie clover (*Petalostemum* spp.) and sage (*Artemisia* spp.). Sweet grass (*Hierochloe odorata*) was burned as incense during native ceremonies invoking the spirits of good, and it was also used as a delicate perfume.

Long summer days must have been pure heaven for the small boys of prairie tribes as they busied themselves with manly sports. Big bluestem (*Andropogon gerardi*) made ideal arrowshafts and when tipped with the spines of hawthorn, the arrows became formidable missiles against frogs and other small prey (Gilmore 1919).

As summer turned to autumn, thoughts turned to winter provisions. In addition to roots and berries, protein-rich seeds and nuts were valuable foods. Seeds of weedy annuals such as goosefoot, knotweed (*Polygonum* spp.) and marsh elder (*Iva* spp.) could be harvested from drying mud flats and similar open habitats. The most valued seed crop came from wild rice (*Zizania aquatica*) although it is found only in the eastern half of the region. Hazelnuts (*Corylus* spp.) and acorns (*Quercus* spp.) were also gathered for food although acorns had to be leached of their bitter tannic acid before they could be eaten (Gilmore 1919, Rogers 1980b).

The cottonwood, a tree invested with mystic powers, flourished in virtually every stream valley. Who could fail to be soothed by the soft rustle of its leaves on a calm day? Whatever the reason for its symbolic importance to the prairie tribes, cottonwood served practical needs. Its inner bark offered emergency food, its fuzzy catkins a chewy treat and its leaf buds a yellow dye. Children enjoyed fashioning the large triangular leaves into miniature tipis, moccasins and toy whistles (Gilmore 1919, Rogers 1980b).

Wooded areas were vital to the survival of prairie tribes. This is reflected in the Western Dakota language - it has 17 different terms for woody habitats (Rogers 1980a). In addition to cottonwood, other common trees were green ash, aspen (*Populus tremuloides*), American/white elm (*Ulmus americana*), bur oak (*Quercus macrocarpa*), box-elder/Manitoba maple, and in the western part of the region, Rocky Mountain juniper (*Juniperus scopulorum*) and ponderosa pine (*Pinus ponderosa*) (Barkley 1977, Wali et al. 1980). Of these, ash and elm were favored for building (Gilmore 1919). Many shrubs were used in crafts. Juneberry/Saskatoon and chokecherry made strong arrow shafts, and sandbar willow (*Salix interior*) was sought for baskets (Rogers 1980b). Virtually all woody species were burned as fuel, although elm was preferred (Gilmore 1919). Conifers were avoided for indoor fires because the resin produced sparks and too much smoke (Laubin and Laubin 1957).

Firewood on the prairie was often in short supply. For example, Denig (1961:81) the mid-19th century fur trader, said of the bison-hunting Assiniboin in western North Dakota: "Owing to the absence of wood on this great plain they are obliged to place their camp on or near the Missouri in the Winter Season." Similarly, the French explorer La Vérendrye had commented on the Assiniboin a century earlier: "They even make the dogs carry wood for fires, frequently being obliged to camp in open prairie, where the islands of timber are distant from one another" (Smith 1980:50).

Firewood and building timber were just as important to the farming tribes as to the hunters. When local supplies were depleted, villages were moved, sometimes every six or seven years (Griffin 1977). A typical farming community would be perched on a high terrace overlooking its fields and the river below (Will and Hyde 1917). Behind it was the open prairie. Such a settlement of several hundred people would be surrounded by a wooden palisade. Inside the walls were earth-covered lodges grouped around a central plaza.

Field crops included squashes and pumpkins (*Cucurbita* spp.), beans (*Phaseolus vulgaris*), sunflowers (*Helianthus annus*) and tobacco (*Nicotiana rustica*), but corn (*Zea mays*) reigned supreme (Wilson 1917, Will and Hyde 1917). Legend made it clear that in the beginning Mother Corn, assisted by animals, led the people out of the ground. She gave the people four ears of corn, each symbolizing the four sacred colours - red, yellow, blue and black. The bond between Mother Corn and the people was a lasting

one. At planting time, some tribes held a ceremony during which each woman was given a few kernels of sacred corn to mix with her own seed grain (Will and Hyde 1917). All of the tribes held harvest ceremonies that usually lasted for several days. In some villages a sacred ear of corn shared the same altar with a buffalo skull, the symbol of animal sustenance (Will and Hyde 1917).

Strong spiritual bonds united the native people, the plants they used and their environment. Black Elk, a Sioux holy man said:

> We are of earth, and belong to You, O Mother Earth from who we received our food, You care for our growth as do our own mothers. Every step that we take upon You should be done in a sacred manner; each step should be a prayer. (In Hughes 1983:20).

19TH CENTURY EUROPEANS

Compared with the slow spread of native agriculture, European practices struck the prairies like a storm. Beginning in the early 1700's and lured by furs, land and adventure, European traders penetrated the northeast via such rivers as the Minnesota, Red, Assiniboine and Missouri. Dozens of fur trading posts sprang up at key points in the communications network amid the fierce competition of the early fur trade (Ray 1974). Later, military forts were built as the pace of colonization quickened and national sovereignty became an issue for both the United States (Robinson 1966, Athearn 1967) and Canada (Morton 1967).

The European immigrants were perhaps as ambivalent towards the prairie as they were toward nature as a whole. In Europe, the 19th century saw an increasing conflict between an exploitative utilitarian view and a growing sympathy for nature (Thomas 1983). While the fur trade was seen by most as merely a livelihood, some objected to it. As early as 1690, the Englishman Thomas Tryon contrasted the native North American's harmonious relation to nature with the negative impact of the European fur traders (Thomas 1983).

To the newcomers, the northeastern prairie posed challenges to overcome although some were impressed by its beauty. In 1690, Henry Kelsey recorded a negative view of the Canadian prairies in doggerel verse:

> This plain affords nothing but Beast and grass and over it in three days time we past (In Warkentin 1964:23).

An 1814 account of the same area:

> Herds of light-limbed antelopes, and heavy colossal buffalo...all these champaign beauties reflected and doubled as it were, by the waters of the river. (Gabriel Franchere and M. Bibaud in Warkentin 1964:110).

Residents of the early posts and forts consumed local fish, game and garden produce, supplemented by imported foodstuffs. Garden plots contained a mixture of European (wheat, cabbage, peas, turnips) and native (corn, beans, squashes) crops (Leechman 1970). In addition to cereals, vegetables and root crops, the Hudson's Bay Company posts also imported seeds of spices and, later, of ornamentals. A host of unwanted weeds also arrived as contaminants in seed grain and by other means. Landscaping with exotic flowers became common. Settlers apparently sought to bring the Old World to the New by importing exotic European species. A nostalgic Red River settler wrote:

> One sadly misses the sweet smelling flowers and glorious roses of Old England, the climbing ivy and many hued creepers, but if the nostrils are not regaled, vision is abundantly favored by the bewildering beauty of the woods and prairie. (Douglas 1959:62).

Europeans adopted some native plant uses, in part because many species were similar to those in the Old World. Fresh greens and fruits supplied a number of nutrients. Nutrients included vitamin C which was vital in preventing scurvy, the scourge of the traders (Rich 1976, Athearn 1967). One prized food not found in Europe was described in an Irishman's letter home in 1832:

> But what flogged all that I had ever seen, was making sugar out of a tree, Mary - not a word of a lie do I tell you;...but where's the use of my telling you anything about it, as you have no sugar trees at home. I remember when you and I thought a shuggar stick, a mighty good sort of thing, never thinking I'd lay my eyes on a shuggar tree. (In MacLeod 1955:11).

Throughout the pioneer period, wood was the basic raw material of everyday living - for fuel, housing, household utensils, farming implements, carts and wagons, furniture and toys. Historical accounts offer insights into the early wood economy but they lack details about species chosen and their relative importance. In such cases, archaeological evidence can fill these gaps. This is illustrated by wood and charcoal from two fur trade posts in southern Manitoba (Fig. 3, Table 3). The uplands surrounding the junction of the Souris and Assiniboine rivers in south-central Manitoba were apparently sparsely wooded in the late 18th and early 19th centuries when several posts were established (Kavanagh 1946). Most wood was hauled from distances in excess of 10 kilometers (6 miles) (Carter nd).

At the junction of the Red and Assiniboine rivers (Fig. 3), timber became scarce in the 1820's shortly after the Red River settlement was established (Keating 1825). By the 1840's, firewood was being hauled from as far away as 100 kilometers (63 miles) (Morton 1950).

Wood and charcoal from archaeological excavations at the mouth of the Souris (Zwiazek and Shay 1984) and from Upper Fort Garry at the Red and Assiniboine junction (Monks 1984, Shay 1984, Shay unpubl.) shed further light on these imports (Fig. 3, Table 3). It seems that much of the timber for building was brought from a distance while local river valley species supplied the firewood. In fact, 60% of the wood pieces found at Upper Fort Garry (Shay unpubl.) must have come from the boreal and conifer-deciduous forests more than 100 kilometers to the south and east (Fig. 2). Such woods included spruce, pine, larch and cedar and/or fir. On the other hand, parkland species were used for fuel. Poplar and/or willow, oak and ash made up 94% of the charcoal sample (Table 3, Shay unpubl.).

ENVIRONMENTAL IMPACTS OF PLANT USES

The lifestyles of the native hunters and gatherers, the native farmers and the European fur traders had different impacts on local vegetation, the spread of wild species and the introduction of exotics. The nomadic buffalo hunters apparently had the least impact on their environment. Apart from their selective harvesting for food, medicine and other purposes, the most dramatic effects on the northeastern prairie probably resulted from prairie fires (Nelson and England 1971). Native tribes set fires for hunting and other purposes although deliberate burning was not universally practiced. Indeed, the Assiniboin explicitly prohibited setting fires (Denig 1930).

The densely-settled farming villages used greater quantities of local firewood and building timber than the nomadic tribes (Griffin 1977). Selective cutting and firewood harvesting must have seriously, if temporarily, depleted local forests.

In contrast, the early fur traders wrought significant changes on the landscape. The depletion of local timber supplies and the spread of exotic European crops and weeds have been mentioned, and these trends accelerated throughout the 19th century with expanding population and settlement. The rapid spread of European plants is well known although botanists have long been intrigued by the idea that native peoples extended the range of certain indigenous species. In 1905, Blankenship suggested that the wide distribution of wild sunflower (*Helianthus* spp.), goosefoot, and marsh elder in Montana was related to their use as food by natives.

TABLE 3. Wood and charcoal from 19th Century fur trade forts in southern Manitoba. The wood and partially-charred wood probably comes from construction and crafts; the charcoal represents the residue of heating and cooking fires.

	Souris Mouth[1] Souris & Assiniboine rivers				Upper Fort Garry[2] Red & Assiniboine rivers			
	Vegetation		Wood	Charcoal	Vegetation		Wood	Charcoal
Tree type	local	>10 km			local	>100 km		
Elm (Ulmus)					x		x	
Ash (Fraxinus)	x		x	x	x		x	x
Box-elder/Maple (Acer)	x				x			
Poplar-Cottonwood (Populus)	x		x	x	x		x	x[4]
Basswood (Tilia)					x		x	
Willow (Salix)					x		x	
Oak (Quercus)		x	x	x	x		x	x
Conifer						x		x
Spruce (Picea)		x	x	x		x	x	
Pine (Pinus)						x	x	
Larch (Larix)		x		x[3]		x	x	
Cedar or fir (Thuja or Abies)						x	x	

1 recent excavations at the junction. Date ca. 1793-1805; n = 74 pieces of wood and partially charred wood, n = 111 pieces of charcoal (Zwiazek and Shay 1984).

2 recent excavations of two privy/refuse pits within the fort, n = 310 pieces of wood, n = 31 pieces of charcoal.

3 identity uncertain. 4 poplar and/or willow.

In 1931, Gilmore discussed the range extension of several eastern plants into the central plains including sweet flag (*Acorus calamus*), black walnut (*Juglans nigra*), prairie crab-apple (*Pyrus ioensis*), and wild plum (*Prunus americana*). The buffalo berry (*Shepherdia argentea*) may have moved eastward when its dried berries were carried from camp to camp (Gilmore 1931).

The problem of past range extensions is one in which botanists and archaeologists can profitably work together. Modern distribution maps of the plains flora (Barkley 1977), coupled with detailed paleobotanical studies (e.g., McAndrews 1966) and analyses of plant remains from archaeological sites (e.g., Benn 1974, Nickel 1977) should help to explain some of these distributions.

POSTSCRIPT

But what of the prairie's future? What of the mines and dams, the power lines and blowing sands? Alvin Josephy (1975) addressed the IVth Prairie Conference on the environmental threats to the northern prairies - huge strip mines and the controversial Garrison Diversion. Both issues are still with us a decade later. Such manifest pressures on the land are not easily reduced and we as a society seem incapable of coping with them. Our prevailing attitude is far from the sacred ties which bound native peoples to the land that sustained them.

Our attitude to and impact on the land was summarized by Aldo Leopold (1966:xix):

> We abuse land because we regard it as a commodity belonging to us. When we see land as a community to which we belong, we may begin to use it with love and respect. There is no other way for land to survive the impact of mechanized man, nor for us to reap from it the esthetic harvest it is capable, under science, of contributing to culture.

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PREHISTORIC SUBSISTENCE-SETTLEMENT PATTERNS IN THE PRAIRIE LAKE REGION

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INTRODUCTION

The purpose of this paper is to examine prehistoric human lifeways in the Prairie Lake region of southwestern Minnesota, eastern South Dakota, and north-central Iowa based on recent data from a number of sites in the region. Although a considerable amount of archaeological work was done in southwestern Minnesota in the mid-twentieth century, it has only been in the last ten years that extensive surveys and excavations utilizing fine-scale recovery techniques have been attempted throughout the region (cf. Anfinson 1982a). The information produced by this archaeological work allows us to investigate economic orientations throughout much of the region at different time periods. This paper will focus on prehistoric subsistence patterns, but includes some discussion of settlement patterns since the two topics are so intimately linked.

The Prairie Lake region (Fig. 1) is a natural area defined by a congruent distribution of tallgrass prairie vegetation and numerous shallow lakes. When compared to the Prairie Pothole region which encompasses most of the northeastern Plains, the limits of the Prairie Lake region are more restricted not only due to the exclusion of the mixed-grass prairie, but an emphasis on fresh water lakes of at least 500 acres in extent whose levels fluctuate only slightly in years of "normal" precipitation and temperature and whose waters are relatively non-alkaline. When doing a cultural study in an area defined by natural boundaries, it is important to remember that human groups are not limited to particular behavioral responses by particular environments, but are presented with a number of possibilities within these environments. Their responses to these possibilities are determined by a complex combination of their attempts to satisfy social as well as natural needs. Understanding why cultures respond the way they do is one of the principal goals of archaeology.

ENVIRONMENT OF THE PRAIRIE LAKE REGION

At the time of white settlement (ca. 1860), the vegetation of the Prairie Lake region was dominated by the grasses and forbs typical of the tallgrass prairie (cf. Weaver 1954, Küchler 1964, Risser et al. 1981). Woody vegetation was not uncommon in the region, but was limited to fire-protected areas near large lakes, rivers and topographic breaks. Following the retreat of the glaciers about 12,000 years ago, a series of forest associations initially revegetated the Prairie Lake region with prairie dominance beginning about 9,000 years ago (Jelgersma 1962, Watts and Bright 1968, Baker and Van Zant 1980).

The lakes of the Prairie Lake region are notable for their shallowness (5'-10' average depth), their number (at least 5,000 of 10 acres or more), their diverse biological richness and their hard water chemistry. Most of the lakes occupy irregularities in the calcareous till of the Des Moines and James glacial lobes (Zumberge 1952, Matsch 1972). Glacial drift covers the entire region, and outcrops of native rock are rare. The two major topographic features of the region are the Coteau des Prairie highlands in the west and the Minnesota River Valley in the region's center.

The climate of the Prairie Lake region features cold winters and warm summers. Freezing temperatures begin in late September and end in early May with the lakes frozen from December to April. Drought is frequent in the Prairie Lake region, and although

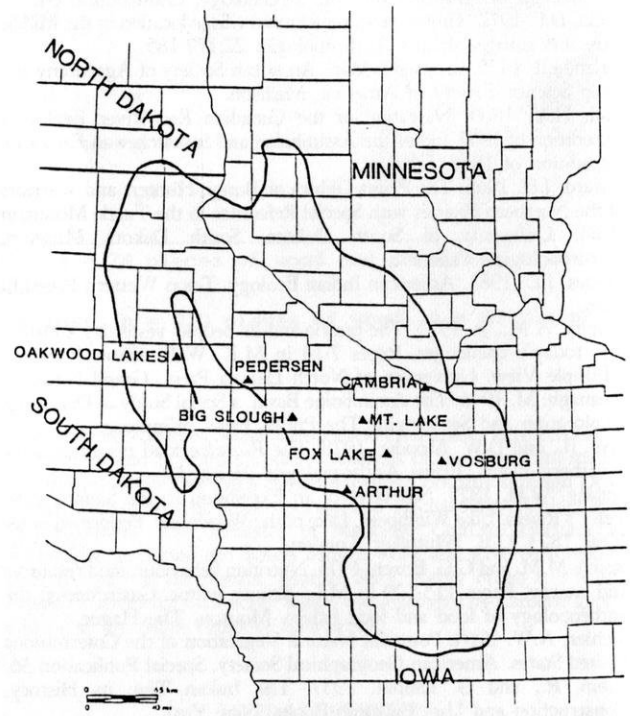

FIG. 1. Extent of the Prairie Lake Region (heavy line) and location of selected archaeological sites (triangles).

the vegetation and topography have been essentially stable for the last 9,000 years, short-term and long-term climatic changes no doubt had significant impacts on human subsistence and settlement in the region; water levels fluctuated, animal populations shifted and cultigens withered or thrived.

CULTURAL HISTORY OF THE PRAIRIE LAKE REGION

Prehistoric human occupation of the Prairie Lake region can be divided into three periods: Early, Middle and Late. The Early Prehistoric period begins with the retreat of the glaciers 12,000 years ago and ends with the appearance of the "classic" Prairie Lake subsistence settlement pattern evident at most of the excavated lacustrine sites. This Early period is poorly understood due to the paucity of sites, especially excavated ones. Lanceolate projectile points typical of the Paleo-Indian tradition have been found only at a few surface sites in the region (Anfinson 1982a:71). Later in the period, stemmed, side-notched, and corner-notched points associated with the Early Archaic tradition may appear in the Prairie Lake region, but well dated, definitive lithic studies of this time period are lacking in the region. The subsistence pattern inferred from excavated sites in adjacent grassland regions is one of focal bison hunting (Anderson and Senken 1980). The settlement pattern has not been determined but may differ from later periods since Early Prehistoric components are uncommon at most Middle and Late prehistoric sites.

The advent of the Middle Prehistoric period about 5,000 years ago is signaled by the location of habitation sites on islands,

peninsulas, and isthmuses at the lakes and a subsistence pattern that emphasizes bison procurement, but includes some reliance on aquatic animals such as fish and muskrat (Anfinson 1982b). Projectile point forms are probably continued from the preceding period and temporally correspond with the Late Archaic forms to the south and east. A major technological innovation, ceramics, appears in the region by as early as 2,500 years ago which marks the beginning of the Initial Woodland phase. The ceramics are called Fox Lake in Minnesota and are typified by thick-walled, conical vessels with cordmarked body exteriors and trailed-line, bossed or punctated decorations on the vessel rim (Anfinson 1979). The other hallmarks of the Woodland Tradition in regions to the east and south, burial mounds and limited horticulture, may not appear in the Prairie Lake region until later.

The Late Prehistoric period in the Prairie Lake region is denoted by a change in the Woodland ceramics and the appearance of horticultural villages on river terraces associated with Plains Village and Oneota peoples (Anfinson 1982a). This happens about A.D. 800. Groups associated with the Terminal Woodland phase appear to continue the basic subsistence-settlement pattern evident in the Middle Prehistoric period while Plains Village (Great Oasis, Cambria) and Oneota groups in the region appear to adapt or adopt elements of the pattern to compliment their horticulture. Burial mounds are in use during this period and may be associated with all cultural groups. Projectile points are smaller denoting a shift from spears to the bow and arrow. The period ends about 500 years ago. During Early Historic times the Prairie Lake region was dominated by the Dakota or Sioux Indians.

PROBLEMS AND METHODS IN SUBSISTENCE STUDIES

The basic problem of subsistence studies is in obtaining a sample that adequately fulfills the requirements necessary to obtain accurate and useful results. Subsistence data from archaeological excavations can suggest inappropriate conclusions if there is misinterpretation of how it was deposited, who deposited it, how it has been transformed since it was deposited, and how representative a portion of the total sample was recovered by the excavation. Ideally, the site to be sampled has either a single component or multiple components which are easily separable, the people represented by the component(s) left representative remains of their complete diet, the remains have been well preserved, and post-depositional disturbances have been minimal.

Archaeological samples are, of course, always far from ideal even when recovered by the best of excavations from the best of sites; prehistoric people rarely behaved in what archaeologists might consider to be ideal ways. The samples do not reflect just availability, but selectivity as well. Faunal and floral remains are not just food remains, but can represent raw materials for tools, clothing, medicine, and rituals. Archaeological sites are not just villages and camp sites, but kill sites, quarry sites, lookout sites, and ceremonial sites. As long as archaeologists are aware of these problems and the recovered sample is applied only to appropriate analyses, results can be useful in reconstructing subsistence-settlement patterns.

This study examines data recovered from eight archaeological sites in the Prairie Lake region. The sites were occupied by peoples of various cultural complexes and are in various topographic locations. Sampling methods varied greatly at the sites as did analytical techniques which produced the data used in this study. Some attempt was made to standardize the comparison of these sites, but as illustrated in Tables 1-3, this was not uniformly possible. A number of conclusions are possible, however, even accounting for the differential recovery and analysis.

With regard to the animal remains recovered from the sites, three categories were employed to compare the sites: Number of Identifiable Elements, Minimum Number of Individuals, and Potential Edible Meat projections. Identifiable Elements are usually bones containing articulating ends which are compared to modern examples in order to determine species. Minimum Numbers for each species are then determined by counting the largest number of examples of a given element from each species (such as right femurs). Potential Edible Meat is then projected based on the available edible meat per animal and average live weights. Some assumptions must be made at this point such as deciding which animals were "edible" and how much of each edible animal was actually eaten. Standard tables have been published giving edible meat projections for common mammals, birds, fish, and reptiles (White 1953, Dallman 1983). The greatest potential for error in these tables is with large mammals, which can differ in weight enormously by age and sex, and with fish since sizes vary so greatly in a given family. Accurate live weight projections for fish can be made based on the sizes of particular elements, and accurate live weight projections for large mammals can be made based on sizes and maturity of elements. Most analyses used by this paper did not project fish and large mammal sizes, however, so unless noted, rough projections were made based on general observations of size (e.g., large, small, immature, mature) and average weights for modern examples. The reader is referred to a number of sources which discuss the problems encountered by utilizing the various methods employed in this paper (Hesse 1982, Dallman 1983, Daly 1969, Grayson 1973, 1978, Stewart and Stahl 1977).

SUBSISTENCE REMAINS FROM SELECTED PRAIRIE LAKE REGION ARCHAEOLOGICAL SITES

Of the eight archaeological sites investigated by this paper, six are in southwestern Minnesota, one in eastern South Dakota, and one in northern Iowa (Fig. 1). All of the sites are village sites and, while most have more than one cultural component, almost all have a dominant component to which most of the remains in Table 1-3 can be attributed. The cultural differentiations at these sites are based primarily on ceramic distinctions.

The Fox Lake site (21 MR 2) is in southwestern Minnesota on Weber Island in Fox Lake near the town of Sherburn. Limited excavations were carried out in 1941, 1981 and 1982 by investigators associated with the University of Minnesota. The site is principally a Woodland habitation with minor Plains Village, Oneota and, perhaps, Late Archaic occupations. Only the 1981-82 faunal materials are represented in Table 1 as the earlier excavation did not employ techniques designed to recover a representative faunal sample.

The Big Slough site (21 MU 1) is near Slayton in southwestern Minnesota on a cultivated hilltop that was formerly an island in a shallow lake. The site was excavated in 1949 and 1950 by the University of Minnesota and again in 1971 by a joint University of Minnesota-University of Nebraska expedition. The site has evidence for Initial Woodland, Terminal Woodland, Oneota, Plains Village (Great Oasis), and possibly, Archaic occupations (Anfinson 1977). Only the 1971 material appears in Table 1 for the same reasons given above for the Fox Lake site.

The Mountain Lake site (21 CO 1) is on a prominent, wooded hill that was an island in a now-drained lake in southwestern Minnesota. The hill is the namesake for the nearby town of Mountain Lake. The University of Minnesota excavated the site in 1957 and the Science Museum of Minnesota excavated there in 1977. Unfortunately, neither excavation attempted any fine-scale recovery methods so most of the fish bone, floral remains, and small mammal remains were lost. The faunal remains from 1977 were analyzed by Shane (1978) and appear in Table 2. There were four cultural components, Late Archaic, Initial Woodland, Terminal Woodland, and Oneota, of which the Woodland components were the most evident.

The Pederson site (21 LN 2) is located on an island in Lake Benton in Lincoln County, southwestern Minnesota. The site was originally tested by the University of Minnesota in 1956, and in 1973 and 1974 the Science Museum of Minnesota undertook extensive excavations there. Evidence for Late Archaic, Woodland

TABLE 1. Potential edible meat for various vertebrate species and results of faunal analyses from the Fox Lake and Big Slough sites. The Fox Lake data is new while the Big Slough data was taken from Anfinson (1982b).

	EDIBLE MEAT(Kg)		FOX LAKE						BIG SLOUGH					
			ID Elem.		Min.No.		Ed. Meat		ID Elem.		Min.No.		Ed. Meat	
	Range	Adult Ave.	#	%	#	%	Kg	%	#	%	#	%	Kg	%
Bison	9-600	450.	21	9.7	2	3.8	600.	82.4	260	49.8	6	14.	2700.	96.1
Elk	5-160	150.	0	0	0	0	0	0	0	0	0	0	0	0
Deer	1.75-55	45.	7	2.9	1	1.9	45.	6.9	2	.4	1	2.3	45.	1.6
Dog/Wolf	1.5-20	10.	5	2.1	1	1.9	10.	1.4	20	3.8	1	2.3	10.	.4
Beaver	1.-17.5	15.	2	.8	1	1.9	15.	2.	3	.6	1	2.3	15.	.5
Muskrat	- -	1.	81	33.5	9	17.	9.	1.2	79	15.1	8	18.6	8.	.3
Racoon	- -	7.9	5	2.1	1	1.9	7.9	1.1	5	1.	1	2.3	7.9	.3
Badger	- -	6.3	4	1.7	2	3.8	12.6	1.7	2	.4	1	2.3	6.3	.2
Skunk	- -	2.3	10	4.1	4	7.5	9.2	1.2	7	1.3	1	2.3	2.3	.1
Otter	- -	5.9	0	0	0	0	0	0	0	0	0	0	0	0
Marten	- -	.8	0	0	0	0	0	0	0	0	0	0	0	0
Gopher	- -	.3	8	3.3	3	5.7	.9	.1	34	6.5	6	14.	1.8	.1
Fox	- -	2.3	5	2.1	1	1.9	2.3	.3	0	0	0	0	0	0
Mink	- -	.5	3	1.2	2	3.8	1.	.1	0	0	0	0	0	0
Rabbit	.7-1.6	1.2	0	0	0	0	0	0	2	.4	1	2.3	1.2	<.1
Gr.Squirrel	.14-.35	.25	0	0	0	0	0	0	2	.4	1	2.3	.25	<.1
Woodchuck	- -	2.1	0	0	0	0	0	0	0	0	0	0	0	0
Porcupine	- -	4.9	0	0	0	0	0	0	0	0	0	0	0	0
Squirrel	- -	.6	0	0	0	0	0	0	0	0	0	0	0	0
TOTAL MAMMAL			151	62.4	27	50.9	712.9	97.9	416	79.7	28	65.1	2797.7	99.6
N. Pike	.25-10.	.5	61	25.2	18	33.	9.	1.2	2	.4	1	2.3	.5	<.1
Bullhead	.05-.9	.25	7	2.9	2	3.8	.5	.1	71	13.6	9	20.9	2.25	.1
Crappie	- -	.25	0	0	0	0	0	0	0	0	0	0	0	0
Perch	- -	.15	0	0	0	0	0	0	0	0	0	0	0	0
Sucker	- -	1.	0	0	0	0	0	0	0	0	0	0	0	0
Gar	- -	.4	0	0	0	0	0	0	0	0	0	0	0	0
Sunfish	- -	.15	0	0	0	0	0	0	0	0	0	0	0	0
Walleye	.25-2.5	.5	0	0	0	0	0	0	0	0	0	0	0	0
Bowfin	.25-2.5	.5	0	0	0	0	0	0	0	0	0	0	0	0
Drum	.25-2.5	.5	0	0	0	0	0	0	0	0	0	0	0	0
Minnow	- -	.02	0	0	0	0	0	0	0	0	0	0	0	0
Buffalofish	.5-10.	1.	0	0	0	0	0	0	0	0	0	0	0	0
Redhorse	.5-7.5	1.	0	0	0	0	0	0	0	0	0	0	0	0
Bass	- -	.4	0	0	0	0	0	0	0	0	0	0	0	0
TOTAL FISH			68	28.1	20	37.7	9.5	1.3	73	14.	10	23.3	2.75	.1
Goose	- -	2.5	1	.4	1	1.9	2.5	.3	1	.2	1	2.3	2.5	.1
Duck	.35-1.1	.7	11	4.5	3	5.7	2.1	.3	5	1.	1	2.3	.7	<.1
Cormorant	- -	1.9	0	0	0	0	0	0	0	0	0	0	0	0
Crane	- -	5.	0	0	0	0	0	0	2	.4	1	2.3	5.	.2
Grouse	- -	.9	0	0	0	0	0	0	0	0	0	0	0	0
Grebe	- -	.3	0	0	0	0	0	0	0	0	0	0	0	0
Heron	- -	2.	0	0	0	0	0	0	0	0	0	0	0	0
TOTAL BIRD			12	5.	4	7.5	4.6	.6	8	1.5	3	7.	8.2	.2
Ptd. Turtle	.25-1.	.5	11	4.5	2	3.8	1.	.1	26	5.	2	4.7	1.	<.1
Snap. Turtle	.5-10.	1.	0	0	0	0	0	0	0	0	0	0	0	0
Soft. Turtle	.5-5.	1.	0	0	0	0	0	0	0	0	0	0	0	0
TOTAL TURTLE			11	4.5	2	3.8	1.	.1	26	5.	2	4.7	1.	<.1
TOTALS			242	100	53	100	728.	100	523	100	43	100	2809.7	100

TABLE 2. Results of faunal analyses from the Mountain Lake (21 CO 1), Pedersen (21 LN 2) and Cambria (21 BE 2) sites. Data from Shane (1978, 1982) and Watrall (1968, 1974).

	MT. LAKE						PEDERSEN						CAMBRIA					
	ID Elem.		Min.No.		Ed. Meat		ID Elem.		Min.No.		Ed. Meat		ID Elem.		Min.No.		Ed. Meat	
	#	%	#	%	Kg	%	#	%	#	%	Kg	%	#	%	#	%	Kg	%
Bison	98	58.	6	12.5	2700.	94.1	108	17.	6	7.1	2700.	92.4	197	?	4	?	1800.	?
Elk	0	0	0	0	0	0	3	.5	1	1.2	150.	5.1	5	?	2	?	350.	?
Deer	2	1.2	1	2.1	45.	1.6	0	0	0	0	0	0	276	?	15	?	675.	?
Dog/Wolf	8	4.7	6	12.5	60.	2.1	7	1.1	3	3.6	30.	1.	107	?	8	?	80.	?
Beaver	2	1.2	1	2.1	15.	.5	0	0	0	0	0	0	102	?	6	?	90.	?
Muskrat	7	4.1	4	8.3	4.	.1	54	8.5	5	6.	5.	.2	4	?	3	?	3.	?
Racoon	3	1.8	1	2.1	7.9	.3	0	0	0	0	0	0	31	?	7	?	55.3	?
Badger	1	.6	1	2.1	6.3	.2	1	.2	1	1.2	6.3	.2	3	?	1	?	6.3	?
Skunk	1	.6	1	2.1	2.3	.1	6	.9	1	1.2	2.3	.1	4	?	2	?	4.6	?
Otter	2	1.2	1	2.1	5.9	.2	2	.3	1	1.2	5.9	.2	6	?	2	?	11.8	?
Marten	0	0	0	0	0	0	1	.2	1	1.2	.8	<.1	0	0	0	0	0	0
Gopher	14	8.3	4	8.3	1.2	<.1	0	0	0	0	0	0	3	?	3	?	.9	?
Fox	1	.6	1	2.1	2.3	.1	0	0	0	0	0	0	4	?	1	?	2.3	?
Mink	0	0	0	0	0	0	1	.2	1	1.2	.5	<.1	1	?	1	?	.5	?
Rabbit	5	3.	3	6.3	6.6	.2	0	0	0	0	0	0	0	0	0	0	0	0
Gr.Squirrel	1	.6	1	2.1	.25	<.1	0	0	0	0	0	0	0	0	0	0	0	0
Woodchuck	0	0	0	0	0	0	0	0	0	0	0	0	3	?	3	?	6.3	?
Porcupine	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Squirrel	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TOTAL MAMMAL	145	85.8	31	64.6	2856.75	99.6	183	28.8	20	23.8	2900.8	99.3	746	?	58	?	3086.	?
N. Pike	7	4.1	3	6.3	1.5	<.1	46	7.2	4	4.8	2.	.1						
Bullhead	9	5.3	6	12.5	1.5	<.1	290	45.6	34	40.5	8.5	.3						
Crappie	0	0	0	0	0	0	3	.5	3	3.6	.75	<.1						
Perch	1	.6	1	2.1	.15	<.1	104	16.4	18	21.4	2.7	.1						
Sucker	0	0	0	0	0	0	1	.2	1	1.2	1.	<.1						
Gar	0	0	0	0	0	0	0	0	0	0	0	0						
Sunfish	0	0	0	0	0	0	0	0	0	0	0	0						
Walleye	0	0	0	0	0	0	0	0	0	0	0	0						
Bowfin	0	0	0	0	0	0	0	0	0	0	0	0						
Drum	0	0	0	0	0	0	0	0	0	0	0	0						
Minnow	0	0	0	0	0	0	0	0	0	0	0	0						
Buffalofish	0	0	0	0	0	0	0	0	0	0	0	0						
Redhorse	0	0	0	0	0	0	0	0	0	0	0	0						
Bass	0	0	0	0	0	0	0	0	0	0	0	0						
TOTAL FISH	17	10.1	10	20.8	3.15	.1	444	69.8	60	71.4	14.95	.5	(646)	?	?	?	?	?
Goose	1	.6	1	2.1	2.5	.1	1	.2	1	1.2	2.5	.1						
Duck	4	2.4	4	8.3	2.8	.1	0	0	0	0	0	0						
Cormorant	0	0	0	0	0	0	0	0	0	0	0	0						
Crane	0	0	0	0	0	0	0	0	0	0	0	0						
Grouse	1	.6	1	2.1	1.3	<.1	0	0	0	0	0	0						
Grebe	0	0	0	0	0	0	0	0	0	0	0	0						
Heron	0	0	0	0	0	0	0	0	0	0	0	0						
TOTAL BIRD	6	3.6	6	12.5	6.6	.2	1	.2	1	1.2	2.5	.1	(79)	?	?	?	?	?
Ptd. Turtle	0	0	0	0	0	0	2	.3	1	1.2	.5	<.1						
Snap. Turtle	0	0	0	0	0	0	6	1.	1	1.2	1.	<.1						
Soft. Turtle	1	.6	1	2.1	1.	<.1	0	0	0	0	0	0						
TOTAL TURTLE	1	.6	1	2.1	1.	<.1	8	1.3	2	2.4	1.5	.1	(504)	?	?	?	?	?
TOTALS	169	100	48	100	2867.5	100	636	100	84	100	2920.25	100	(1975)	100	?	100	?	100

TABLE 3. Results of faunal analyses from the Vosburg (21 FA 2), Arthur (13 DK 27) and Oakwood Lakes (39 BK 7) sites. Data from Dobbs (1984), Tiffany (1982) and Hannus (1981).

	VOSBURG						ARTHUR						OAKWOOD LAKES					
	ID Elem.		Min.No.		Ed. Meat		ID Elem.		Min.No.		Ed. Meat		ID Elem.		Min.No.		Ed. Meat	
	#	%	#	%	Kg	%	#	%	#	%	Kg	%	#	%	#	%	Kg	%
Bison	1	.1	1	.7	450.	50.9	112	?	6	1.7	2700.	86.9	270	15.5	19	8.2	8550.	97.2
Elk	15	1.6	1	.7	150.	17.	1	?	1	.3	150.	4.8	2	.1	1	.4	150.	1.7
Deer	21	2.2	2	1.4	90.	10.2	1	?	1	.3	45.	1.4	1	.1	1	.4	45.	.5
Dog/Wolf	50	5.2	4	2.7	40.	4.5	6	?	2	.6	20.	.6	4	.2	1	.4	10.	.1
Beaver	59	6.2	2	1.4	30.	3.4	8	?	2	.6	30.	1.	1	.1	1	.4	15.	.2
Muskrat	4	.4	1	.7	1.	.1	35	?	12	3.4	12.	.4	0	0	0	0	0	0
Racoon	9	.9	2	1.4	15.8	1.8	3	?	3	.9	23.7	.8	0	0	0	0	0	0
Badger	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Skunk	1	.1	1	.7	2.3	2.6	0	0	0	0	0	0	0	0	0	0	0	0
Otter	5	.5	2	1.4	11.8	1.3	7	?	3	.9	17.7	.6	0	0	0	0	0	0
Marten	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gopher	14	1.5	4	2.7	1.2	.1	12	?	6	1.7	1.8	.1	? 5	.3	5	2.2	1.5	<.1
Fox	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mink	3	.3	1	.7	.5	.1	2	?	1	.3	.5	<.1	0	0	0	0	0	0
Rabbit	0	0	0	0	0	0	1	?	1	.3	1.2	<.1	1	.1	1	.4	1.2	<.1
Gr.Squirrel	9	.9	2	1.4	.5	.1	0	0	0	0	0	0	? 1	.1	1	.4	.25	<.1
Woodchuck	1	.1	1	.7	2.1	.2	0	0	0	0	0	0	0	0	0	0	0	0
Porcupine	1	.1	1	.7	4.9	.6	0	0	0	0	0	0	0	0	0	0	0	0
Squirrel	1	.1	1	.7	.6	.1	0	0	0	0	0	0	0	0	0	0	0	0
TOTAL MAMMAL	194	20.3	26	17.7	800.7	90.6	188	?	38	10.9	3001.9	96.6	285	16.4	30	12.9	8772.95	99.7
N. Pike	1	.1	1	.7	.5	.1	?	?	82	23.6	32.33	1.	3	.2	3	1.3	1.5	<.1
Bullhead	617	64.5	86	58.5	21.5	2.4	?	?	40	11.5	6.49	.2	1083	62.2	62	26.7	15.5	.2
Crappie	0	0	0	0	0	0	?	?	8	2.3	2.	.1	0	0	0	0	0	0
Perch	0	0	0	0	0	0	?	?	34	9.8	5.1	.2	4	.2	3	1.3	.45	<.1
Sucker	4	.4	1	.7	1.	.1	?	?	1	.3	1.	<.1	0	0	0	0	0	0
Gar	22	2.3	2	1.4	.8	.1	?	?	5	1.4	2.16	.1	1	.1	1	.4	.4	<.1
Sunfish	8	.8	2	1.4	.3	<.1	?	?	15	4.3	1.11	<.1	35	2.	6	2.6	.9	<.1
Walleye	1	.1	1	.7	.5	.1	?	?	26	7.5	13.	.4	0	0	0	0	0	0
Bowfin	1	.1	1	.7	.5	.1	?	?	2	.6	1.	<.1	0	0	0	0	0	0
Drum	1	.1	1	.7	.5	.1	?	?	2	.6	1.	<.1	0	0	0	0	0	0
Minnow	0	0	0	0	0	0	?	?	1	.3	.02	<.1	323	18.6	121	52.2	2.42	<.1
Buffalofish	2	.2	1	.7	1.	.1	0	0	0	0	0	0	0	0	0	0	0	0
Redhorse	39	4.1	11	7.5	1.	.1	0	0	0	0	0	0	0	0	0	0	0	0
Bass	63	6.6	10	6.8	47.2	5.3	?	?	92	26.4	37.78	1.2	0	0	0	0	0	0
TOTAL FISH	759	79.3	118	80.3	74.8	8.5	?	?	308	88.5	102.99	3.3	1449	83.2	196	84.5	21.17	.2
Goose	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Duck	0	0	0	0	0	0	0	0	0	0	0	0	4	.2	3	1.3	2.1	<.1
Cormorant	2	.2	1	.7	1.9	.2	0	0	0	0	0	0	0	0	0	0	0	0
Crane	1	.1	1	.7	5.	.6	0	0	0	0	0	0	0	0	0	0	0	0
Grouse	0	0	0	0	0	0	0	0	0	0	0	0	1	.1	1	.4	.9	<.1
Grebe	0	0	0	0	0	0	0	0	0	0	0	0	1	.1	1	.4	.3	<.1
Heron	0	0	0	0	0	0	0	0	0	0	0	0	1	.1	1	.4	2.	<.1
TOTAL BIRD	3	.3	2	1.4	6.9	.8	0	0	0	0	0	0	7	.4	6	2.6	5.3	.1
Ptd. Turtle	1	.1	1	.7	.5	.1	?	?	1	.3	.5	<.1	0	0	0	0	0	0
Snap. Turtle	0	0	0	0	0	0	?	?	1	.3	1.	<.1	0	0	0	0	0	0
Soft. Turtle	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TOTAL TURTLE	1	.1	1	.7	.5	.1	?	?	2	.6	1.5	<.1	0	0	0	0	0	0
TOTALS	957	100	147	100	882.9	100	?	?	348	100	3106.39	100	1741	100	232	100	8799.6	100

(Initial and Terminal), Oneota and, perhaps, Plains Village (Cambria) components were recovered (Hudak 1974, 1976). Excavation techniques did not emphasize but included some fine-scale recovery. Only the Initial Woodland faunal remains from the 1970's excavations have been analyzed (Shane 1982) and these results appear in Table 2.

The Cambria site (21 BE 2) is located on a terrace of the Minnesota River, fifteen miles northwest of Mankato in southern Minnesota. The terrace sits about 15 meters above the floodplain and is bisected by a ravine giving the site a steep slope on three sides. A number of archaeological expeditions have tested the Cambria site beginning with W.B. Nickerson in 1913 and 1916. The University of Minnesota worked at the site in 1938, 1941, and 1974. Only the 1974 excavation, the most limited, attempted any fine-scale recovery. The site is basically a single component Plains Village (Cambria) occupation with some Woodland remains (Knudson 1967). Watrall's (1968, 1974) analyses of the faunal materials from the 1913, 1916, 1938, and 1941 excavations are depicted in Table 2.

The Vosburg site (21 FA 2) is in a plowed field on a low terrace of the Blue Earth River at the junction of Center Creek near Winnebago, Minnesota. The University of MInnesota tested the Vosburg site in 1938, 1941, and 1979. It and the adjacent Humphrey site are the type sites for the Blue Earth phase of the Oneota tradition. In a recent analysis, Dobbs (1984) contends that the Vosburg site was a horticultural village occupied intermittently from A.D. 1000 to perhaps early-historic times (ca. 1700), although the radiocarbon dates cluster around A.D. 1300. The 1979 excavations included some fine-scale recovery and the faunal totals for that year's excavation are presented in Table 3.

The Arthur site (13 DK 27) is on an abandoned beach strand on the east side of East Lake Okoboji, two miles southeast of the town of Spirit Lake in northern Iowa. Extensive archaeological testing was done at the site in 1980 to assess and mitigate the impact of sewer construction (Tiffany 1982). The site is multi-component with possible Early Prehistoric, Woodland (Initial and Terminal), Plains Village, and Oneota remains. Woodland remains are most common. Some fine-scale sampling was undertaken. The results of the faunal analyses (Semken 1982, Vondracek and Gobalet 1982) are presented in Table 3.

The Oakwood Lakes site (39 BK 7) is located on an isthmus between Lake Tetonkaha and Oakwood Lake about thirteen miles northwest of Brookings in eastern South Dakota. The site was excavated in 1979 to mitigate the adverse effects of a shoreline stabilization project (Hannus 1981). The site had a major Initial Woodland component and minor Oneota, Plains Village, and Terminal Woodland components. The subsistence remains were analyzed by a number of researchers (Haberman 1981a, 1981b, Semken and Sartorius 1981, Artz 1981, Alex 1981, Riggle 1981).

Tables 1-3 illustrate a number of patterns with regard to prehistoric subsistence patterns in the Prairie Lake region. All of the sites produced a great diversity of species, especially small and medium-sized mammals. Bison was very important at the sites with major Woodland components, while the two sites with major Oneota and Plains Village components had lesser numbers of bison and considerable amounts of deer. (These two site are also the easternmost where bison were probably more scarce.) All of the sites had limited amounts of waterfowl remains which was somewhat surprising considering the great numbers of these birds present in the region. The lack of elk is also surprising.

A more detailed examination of cultural-temporal subsistence trends indicates that there is little species diversity in the pre-Woodland component at the Mountain Lake site where bison and *Canis* sp. bones predominate (Shane 1978), but the small sample is not necessarily representative. While bison predominate Woodland horizons at the lacustrine sites, muskrat and fish are also quite important. Bullheads and northern pike are the most common fish. Floral remains are rare in direct association with Woodland levels. Late Prehistoric components representing horticultural peoples (Oneota, Plains Village) often yield maize, beans, and sunflower remains, especially at riverine sites. Deer are important, along with fish and a diveristy of small mammals. There is also some evidence for increased mussel utilization.

SUMMARY AND CONCLUSIONS

In reviewing the archaeological and historical literature, it is clear that bison have been an important element in the diet of the aborignial peoples of the Prairie Lake region from the Early Prehistoric until the time of intensive white settlement. One gets the impression from the literature, however, that other animals, native plants, and horticultural products simply supplemented bison. This paper suggests that a wide diversity of species were important to prehistoric inhabitants of the Prairie Lake region. Seasonal, yearly, and geographical variations in availability suggest a dependence on any one species would not be a practical subsistence orientation within the region (cf. Lensink 1984). Cultural factors, such as predator-prey relationships (e.g., no hunting during mating season) and seasonal preferences, may also have reduced dependence on bison.

The predominance of bison in the existing archaeological record is no doubt overemphasized by the more complete recovery of large mammal remains by large mesh dry screening (the most common method) and the assumption that all the edible meat of a single bison was used even when only a single element was recovered. It is more likely that a higher percentage of edible meat was used from smaller animals (e.g., fish) since most of the animal could be added to a stew pot with minimal preparation while bison were often killed some distance from a base camp and only a portion of the edible meat carried home.

Another possible misinterpretation of the subsistence-settlement pattern of the Prairie Lake region involves season of occupation for particular sites. It is a common practice to infer site seasonality on the presence of certain species (e.g., fish, waterfowl) or the maturity of certain individuals (e.g., bison, deer). While the presence of warm season species or newborn bison may document that a site was indeed occupied during the warm season, it does not mean that the site was not occupied during the winter. Unfortunately, there are no species in the Prairie Lake region which are only available in winter.

The lack of native floral remains from Prairie Lake region sites is no doubt more a matter of preservation and recovery than non-use. The Dakota used a variety of prairie plants quite intensively during particular seasons (Winchell 1911:496). The prairie turnip is an important example. Plant remains usually are not preserved unless well-charred and the seeds of many native plants are not recovered unless the excavated soil is subjected to flotation and fine-mesh screening.

With regards to settlement locations, it is probable that the earliest inhabitants of the Prairie Lake region had a settlement pattern somewhat different from the inhabitants of Middle Prehistoric times onward. It is rare to find an Early Prehistoric horizon at major village sites occupied during Middle and Late Prehistoric times. Unlike adjacent regions to the west, south, and east, the scarcity of these early sites cannot be attributed to deep burial since alluvial, colluvial, and Aeolian deposition in the Prairie Lake region is not extensive. Most soil profiles do not extend much more than a meter before encountering glacial till. Low population density is the best explanation for the lack of early sites. A few lithic sites have recently been found on now-drained lake bottoms (Hudak 1980, Lofstrom 1981) indicating possible settlement locations during periods of severe drought when small water holes may have been present in mostly dry basins. Such conditions may have been most common during the Hypsithermal climatic period which peaked about 6,000 years ago.

The location of non-horticultural villages on lacustrine islands, peninsulas, and isthmuses during the Middle and Late Prehistoric periods can be explained by the presence of a single resource, wood,

but the natural defensive advantages these locations offered with regard to enemy attack and prairie fires cannot be ignored. Most sites on large islands would only be unfavorable locations during the freezeup and thawing of the lakes when they would be difficult to reach or leave. Late Prehistoric horticultural villages in the Prairie Lake region are almost always located on river terraces where nearby river bottom gardens would have been both well-watered and easily cultivated.

Substantial climatic changes have often been cited as primary causes of cultural change, especially in the Plains (e.g., Henning 1968). Drought has drastic effects on the environment of the Prairie Lake region causing many lakes, sloughs, and rivers to almost totally dry up. Severe droughts are not uncommon in the region, appearing at least once every thirty years or, perhaps, several times in a human lifetime. While these droughts would have restricted the availability of drinking water, reduced aquatic animal populations, and increased the incidence of prairie fires, the long-term inhabitants of the Prairie Lake region no doubt had subsistence-settlement patterns adapted not to a static environment but a changing one. A long-term drought put stress on the system, but would not cause its abandonment and may have even increased certain resources such as bison. On the other hand, a series of recurring severe droughts around 500 years ago, a time coincidental with significant cultural changes throughout the Midwest, seems to have caused a reduction in population density in the Prairie Lake region because people at that time were more dependent on cultigens, a resource that is especially drought sensitive.

In conclusion, it has long been apparent that most major Middle Prehistoric villages in the Prairie Lake region are found on lakes, while most major Late Prehistoric horticultural villages are found on river terraces. It has also been common knowledge that bison played an important role in prehistoric subsistence in the region. What has not been stressed is that the above observations do not in any way define subsistence-settlement patterns for the region nor do they explain why people were eating what they were and living where they were.

This paper has tried to illustrate that our understanding of prehistoric lifeways in the region is very tenuous and in order to make it less tenuous we must pay more attention to a number of factors, the most important of which are comprehensive surveys to find where sites are and are not, the employment of fine-scale sampling techniques when we excavate sites to recover representative subsistence remains, and the development of a sound radiocarbon chronology allowing us to make temporal comparisons. Only when such information is available will we be able to accurately reconstruct subsistence-settlement patterns in the region and, perhaps, understand how changes in these patterns reflect or cause cultural changes with respect to a group's social or ideological orientation.

This paper does, however, illustrate that enough information is now available to document that a way of life was established in the Prairie Lake region by the end of the Early Prehistoric (ca. 3000 B.C.) that featured a diverse economy utilizing both upland and aquatic resources. This way of life remained substantially unaltered for perhaps 4,000 years until efficient horticulture begins in the region (ca. A.D. 900). Even the horticulturalists adapted or adopted substantial portions of the Middle Prehistoric subsistence-settlement pattern obviously recognizing how well suited the pattern was to the Prairie Lake environment.

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THE SISSETON-WAHPETON DAKOTA INDIAN FUR TRADES, 1820-1838

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Abstract. A variety of strategies were used by Europeans and American Indians in the Sisseton-Wahpeton regional fur trades, 1820-1838, as a result of the changing environment and available local natural resources. A comparison of the Big Woods riverine Sisseton-Wahpeton and the Prairie Lake patterns bears this out. Patterns of periodicity and seasonality were present. There was a difference between the essential and non-essential fur goods and the percentage used in the Indian society. Changes are evident in the switch from a predominantly beaver fur trade to a muskrat fur trade and then to a robe trade in this period. After eighteen years of contact with the Euro-American colonial economic system, the Dakotas were becoming enmeshed into the Euro-American economic system.

INTRODUCTION

This paper deals with the Dakota Indian fur trade between 1820 and 1838 and its relationship with other indigenous and Euro-American fur trades mainly involving the Hudson's Bay Company, the Northwest Company, the American Fur Company and the Columbia Fur Company, in the cultural region occupied by the Sisseton-Wahpeton Dakota Indians. This geographic area consists mainly of central and southern Minnesota, northern Iowa and the Dakotas. The Euro-American fur trade in the cultural research area of the Sisseton-Wahpeton Dakota Indians between 1820 and 1838 reflected in many ways their annual subsistence strategies.

The cultural adaptation which took place among the Santee Dakota before 1820 was basically an amalgamation of bands coopted into subtribes. In 1820 the Sissetons were divided into two subtribes: the Northern and the Southern. The Wahpetons were divided into two subtribes: the Eastern and the Western.

By 1820 the traditional Sisseton-Wahpeton Dakotas were living in bimodal villages and were exploiting the flora and fauna of the transitional prairie-forest ecotone along the Minnesota River Valley. During the expedition of Major Stephen H. Long, Joseph Renville, Jr., reported the total demography of the Sisseton-Wahpeton as 410 lodges, 950 warriors, and 3,400 persons (Keating 1959).

The Wahpeton and Sisseton summer villages from the junction of the Minnesota and Mississippi Rivers towards Big Stone Lake in 1820 were:

1. Eastern Wahpeton village at Little Rapids or *Inyan-ce-ya-ka-o-ton-we* under Red Eagle or Red Quillon;
2. Eastern Wahpeton village at Belle Plaine, village of the shinney or lacrosse game, Wahpetons of the round prairie;
3. Eastern Wahpeton village at LeSueur, village of the alder thickets;
4. Eastern Wahpeton village at Jordan, village of the sand prairie or sand creek, *Wi-ya-ka-o-ti*;
5. Southern Sisseton village at Traverse des Sioux, village under Red Iron;
6. Southern Sisseton village at Swan Lake under Sleepy Eye, (Durand 1981);
7. Southern Sisseton village at mouth of Little Rock Creek;
8. Western Wahpeton village at Lac qui Parle, moved from Little Rapids village after 1800;
9. Western Wahpeton village at Big Stone Lake under Yellow Spider and Southern Sisseton village at Big Stone Lake under Sweet Corn, (Seymour 1823);
10. Northern Sisseton village on Lake Traverse;
11. Five Lodges or *tizaptan* band of Sissetons, at Two Woods Lake in South Dakota, (Riggs 1839).

The Dakota, like the Lakota believed in the circle as their most important symbol of life (Geertz 1973). Their annual subsistence cycles were also circular (Fig. 1).

The annual seasonal cycle of the Eastern Wahpetons along the lower Minnesota River Valley in 1820 began in the large circular summer villages on grassy areas surrounded by gallery forests. Nearby women planted fields of corn, beans and squash. In the spring the women gathered maple sugar at *chanhassen* or the place of the grey bark trees. In the spring, summer and fall men fished for rock sturgeon in the Minnesota River. Men hunted elk, bear, and deer in the Big Woods, spring, summer and fall. Muskrat and beaver were trapped and speared in the rivers and lakes, spring and fall. In the fall, women gathered wild rice in the local lakes and sloughs especially *psin mde* west of Shakopee and around Lake Minnetonka. In the winter they lived in large villages in the river bottoms or in the Big Woods area west of the Minnesota River.

The Southern Sissetons in the Lower Minnesota River Valley in 1820 lived in large circular villages on the island and shores of Swan Lake. The men hunted muskrat and beaver in the prairies of southern Minnesota. The women gathered wild rice, roots, forbs, wild fowl eggs, turtle and frogs in the wet prairies of southern Minnesota. The men fished for rock sturgeon in the Minnesota River and Rock Creek. They wintered in large circular villages in the Blue Earth River Valley.

The Western Wahpetons lived at Lac qui Parle in large circular summer and winter villages. Mary Riggs' map (1837) showed the summer village of *tipitankas* in the prairie area on the second terrace was surrounded by gallery forests on the south and protected by the bluffs of the river on the northern side. The winter village of *tipis* appeared in heavy timber on the riverine bottom.

The Western Wahpetons used round hide *tipis* migrating in their annual subsistence cycles between summer and winter villages. In the spring in the prairie-forest ecotone of the Minnesota River Valley, they exploited a large variety of food resources including the sap of the box-elder trees. Women planted corn, beans and squash near their summer villages. They moved from the wooded areas along the river, across the wet prairies to the Big Woods area around Otter Tail Lake in search of game for food and furs. On the prairies in the summer, women gathered wild forbs, grasses and berries. In the fall in the wet prairies women gathered wild rice, turtle, wild fowl eggs, fish, frogs, muskrats and birds. In the Big Woods they gathered acorns, fruit, berries, nuts, grapes and wild beans, while the men hunted deer, bear, fishers, foxes, raccoons, elk, mink and martens.

The Northern Sissetons at Lake Traverse practiced primitive horticulture - planting corn seeds in the ground and abandoning the fields - while gathering forbs, grasses, roots, berries, and hunting the buffalo. They wintered on the points and islands in Lake Traverse.

THE SISSETON-WAHPETON FUR TRADES, 1820-1838

Between the years 1820 and 1838 there were four different types of Indian fur trades that were prevalent:

1. The indigenous trading system;
2. The Euro-American trader at an annual Indian fair;
3. The Euro-American fur post close to an Indian village; and
4. The Euro-American trader who traveled by horse and wagon to a village for the robe trade.

The indigenous trading system which developed in the historic period was based upon an empirical economic exchange, i.e., barter, reciprocity and redistribution. The historical Santee Dakota empirical economic exchange system had two parts to it: the internal system and the external system. The internal system was divided into four subsystems:

1. The interpersonal system based upon individual bartering within the village;
2. The intravillage system based upon the *tiospaye* or band system of exchange. In this redistributive society, the bands collected, produced and redistributed resources to their members and other members of the village, including food, shelter and clothing at certain ceremonial occasions, celebrating rites of passage;
3. The intervillage system based upon exchanges between small hunting and gathering groups form different villages;
4. The intratribal system based upon the annual trading fairs held twice annually, summer and winter for the *Oceti Sakowin*: All Dakota, Nakota and Lakota tribes (Grobsmith 1981). The *Oceti Sakowin* or Seven Council Fires met twice a year to exchange ideas, crafts, foods, pipes, women, ornaments and weapons of warfare (Fig. 2). The place of the fair in 1820 was the Oakwood Settlement on the James River. The annual fairs were a time for reorganizing the bands in each village under a headman or headwoman called an *itancan* or "wearer of the shirt." Annually at these fairs marriages took place on an exogamous village basis. Tribal hunting parties were organized in the summer and band hunting parties organized in the winter. During the annual fairs, 160 headmen sat in

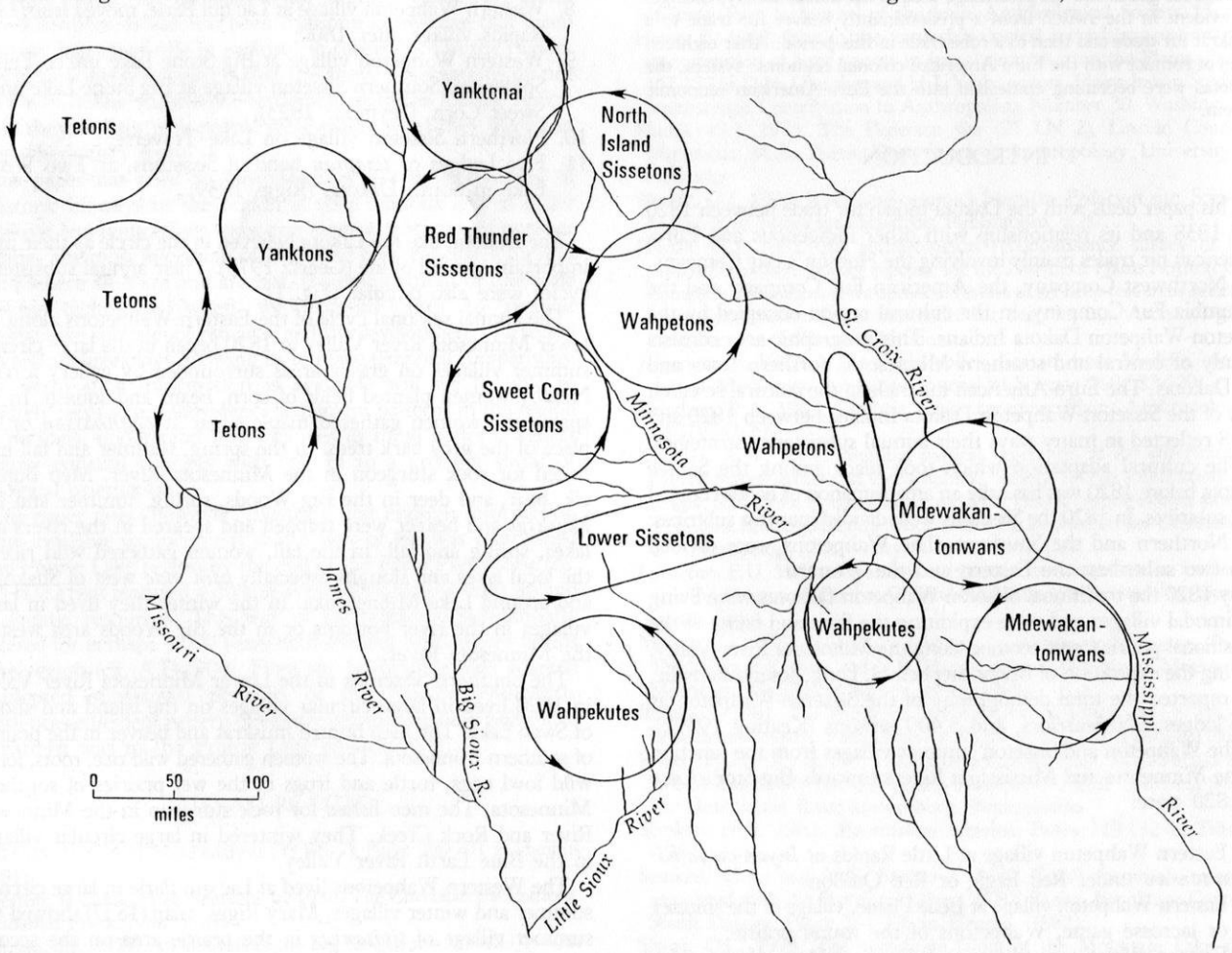

FIG. 1. Annual Sioux subsistence cycles, 1820-1834.

council and planned for the next year. Four headmen were usually chosen to lead the discussion. One headman was usually elected the spokesman for the whole council, who would make alliances and/or establish trade with outsiders.

The external empirical economic exchange system was divided into two subsystems: the intertribal trading systems and the long distance trading system. The intertribal trading system consisted of villages trading on their borders with other tribes for goods, women and warfare alliances. The long distance trade consisted of traders or fictive kin travelling long distances to primary continental trading centers such as those located at Sault Ste. Marie or the Missouri River villages of the Mandan, Hidatsa or Arikara to obtain the luxury items like corn seeds and tobacco.

The European economic colonial trading system by 1820 was based mainly upon the exploitation of the Indian as a cheap producer of raw materials for the large centralized American and European markets. Berkhofer (1965) has stated that the Indian trapper was an agent for a colonial system which stretched from the local post, to the depot, then to national markets in Philadelphia, New York and Boston to Montreal, Quebec and overseas to international markets.

The European colonial spheres of influence in 1820 were vested in wooden fur trading posts near winter villages built by American, British and Canadian companies. By this time the Santee Dakota were entering into the first phase of the American fur trade, with sites of posts at Mendota, Little Rapids, Lac qui Parle, Big Stone Lake, Lake Pepin, and Traverse des Sioux - all dependent upon Prairie du Chien as a depot (Bailly Papers, Minnesota Historical Society). The Hudson's Bay Company had a fur post at the northern side of Lake Traverse attached to Pembina, Grand Forks, Red Lake and Rupert's land at Fort Garry (Bourke's Diary, 1819-20).

By 1820 the beaver populations had been overexploited in the Red River Valley so that the Hudson's Bay Company traders under Duncan Graham of Graham's Point on the Bois des Sioux River in 1819-1820 built a post to trade with the Dakota living at Lake Traverse. But the game hunted and trapped by the Sisseton-Wahpeton Indians for furs winter, spring and fall in the ecotone between the deciduous forests of the Big Woods and the tall grass prairie in western Minnesota were mostly muskrats (Hudson's Bay Company Archives, B.108, d.8, fo. 4-5, Fig. 3).

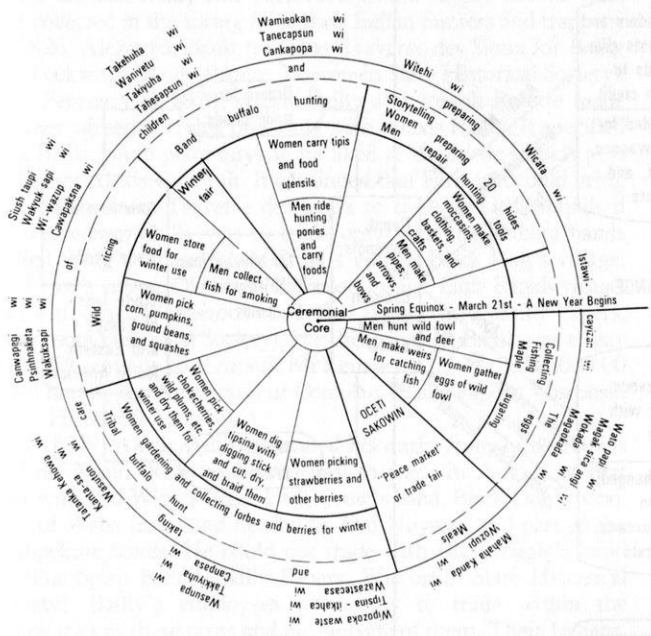

FIG. 2. Ergograph of Wahpeton annual cycle before 1834.

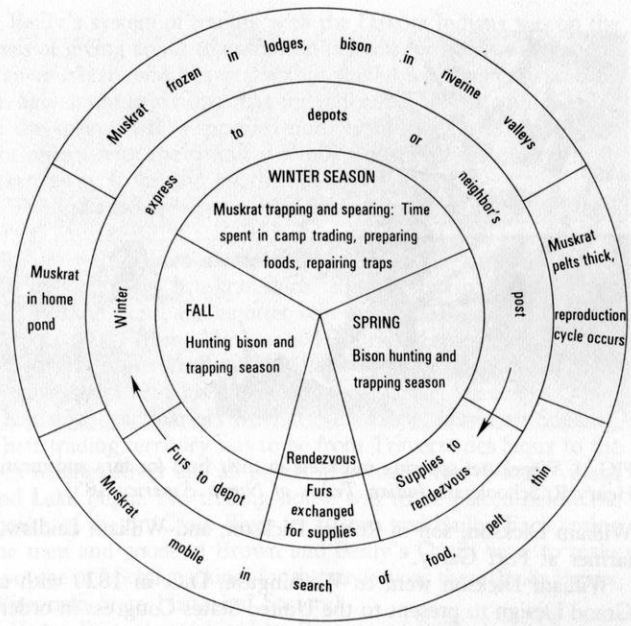

FIG. 3. Annual cycle of operations of American Fur Company, 1820-1834.

Occasionally a Santee Dakota band wandered into the Hudson' Bay Company post, the chief was given some rum and he turned over all of his band's furs to the clerk in return for trade goods, which would resupply their hunting and trapping needs (Hudson's Bay Company Archives, B.108, d.8, fo.3). Almost all the supplies or trade goods given to this band were hunting equipment, including powder, shot, knives, balls, guns, steels, leggings and a capot. Only a few items were non-essential for hunting, like tobacco and looking glasses (Hudson's Bay Company Archives, B.108, d.8, fo.3). The three looking glasses however, were only partially non-essential items, because the hunters would fix their hair and paint their faces before going hunting.

Most of the large quantity of fur trading goods at Graham's Point, 1819-1820, went to voyageurs and their Indian families, and to local Indian chiefs for gifts. Large quantities of goods were given to the Mdewakantonwan relatives of Duncan Graham and Joseph Renville, Jr. (Sibley Papers 1850).

Hazen Mooers and Dennis Robinson in 1819 built two American Fur Company posts in western Minnesota. Sent out in 1818 by James H. Lockwood, Mooers and Robinson moved in the spring of 1819 into posts at Lac qui Parle and Big Stone Lake. Lockwood also sent Duncan Campbell to a trading post at the mouth of the Minnesota River; Scott Campbell to a trading post at Traverse des Sioux; and Augustin Rocque to a wintering post at Lake Pepin (Sibley Papers, roll No. 1).

The American Fur Company was organized in 1820 at Prairie du Chien to collect furs and distribute goods to their winterers. The main depot was on Pike's Island under the *bourgeoise* Jean Baptiste Faribault. The furs were gathered by Indian hunters and trappers in the winter and spring at the muskrat lodges with spears and axes (Fig. 4). The pelts were traded at the wintering posts in the spring for European manufactured goods.

Muskrat furs were selling very cheaply on the market in the 1820's. The skins at Lac qui Parle, Big Stone Lake, Traverse des Sioux and Little Rapids were selling 20 cents a piece. The skins from Little Rock Creek, Patterson Rapids, Upper Des Moines River and Talbot Lake were selling for 17 cents a piece (Sibley Papers, roll No. 1).

The Hudson's Bay Company pulled out of Lake Traverse in 1822. In 1821, with the union of the North West Company and the Hudson's Bay Company, many of the North West Company employees found themselves unemployed. Among those released were Kenneth McKenzie, former head of the Fort William depot;

FIG. 4. Wapekutes spearing muskrats in their huts for furs and meat. Henry R. Schoolcraft. *Indian Tribes of North America* 1853.

William Dickson, son of Robert Dickson; and William Laidlaw, farmer at Fort Garry.

William Dickson went to Washington, D.C. in 1820 with a Grand Design to present to the United States Congress in order to receive monetary support from the government to develop a new American fur company in the west. The company was to be called the Columbia Fur Company. Dickson presented his design locating the mainpost at Lake Traverse in Robert Dickson's old post. The company's territory was to stretch east down the Minnesota River to the Mississippi River and up the St. Croix River to the Falls. It would extend west among Tetons and into the main villages of the Mandans at the juncture of the Knife and Missouri Rivers. Eventually the plan was to expand the company's posts to the sources of the Missouri River and then west to the Columbia River (Lavendar 1969).

McKenzie, Laidlaw and Lamont declared their intentions of becoming United States citizens. They organized the new company with two other United States citizens - namely William P. Tilton and S.S. Dudley. They contracted with Stone, Bostwick and Company in St. Louis to supply them with Euro-American manufactured goods (Lavendar, 1969). They built a new post in 1822 at Lake Traverse and one in 1823 at Pierre, South Dakota called Fort Tecumseh. By 1826 there was a Fort Adams at Lac qui Parle under Joseph Renville, Jr.; Fort Columbia on the Sheyenne fork of the Red River under William Dickson; Fort Washington at Lake Traverse under William Dickson; Fort Union at Traverse des Sioux under Duncan Campbell; Columbia Fur Company Factory at Land's End near Fort Snelling under Daniel Lamont; a post at St. Croix Falls and Prescott, Wisconsin under Philander Prescott; and a post at Leaf Lake (Parker 1950).

The American Fur Company established Joseph Rolette, Jr., as *bourgeoise* at Prairie du Chien in charge of the Upper Mississippi Outfit and intended to use Dennis Robinson and Hazen Mooers to undercut Dickson and McKenzie's prices in obtaining furs from the Indians. Mooers was sent to winter at the Sheyenne fork of the Red River; a voyageur was sent to Devil's Lake to winter; Louis Provencalle was still trading at Little Rapids; Ezekial Lockwood was trading at Lac qui Parle; Jean Baptiste Faribault was at Mendota; and Dennis Robinson was wintering at Lake Traverse (U.S. Serial No. 93, 1853). Ramsey Crooks placed Renville's post in the northern department and sent Renville's relatives to a post built by Rolette at Whitewood Lake and the James River (Lavendar 1969).

In 1822, Tilton and Dudley received a license to trade with the Sioux at Fort Snelling along the Minnesota River and with the Mandans, Hidatsa and Crow Indians on the Upper Missouri, from William Clark at St. Louis. In the fall of 1822, Tilton left Lake Traverse with horses and wagons for the Missouri River villages of the Mandans under Joseph Jeffries, James Kipp and three other men. Their intention was to establish a fort among the Mandans and to gather up all the buffalo robes, plus the produce of the country and to carry them back in wagons to Lake Traverse

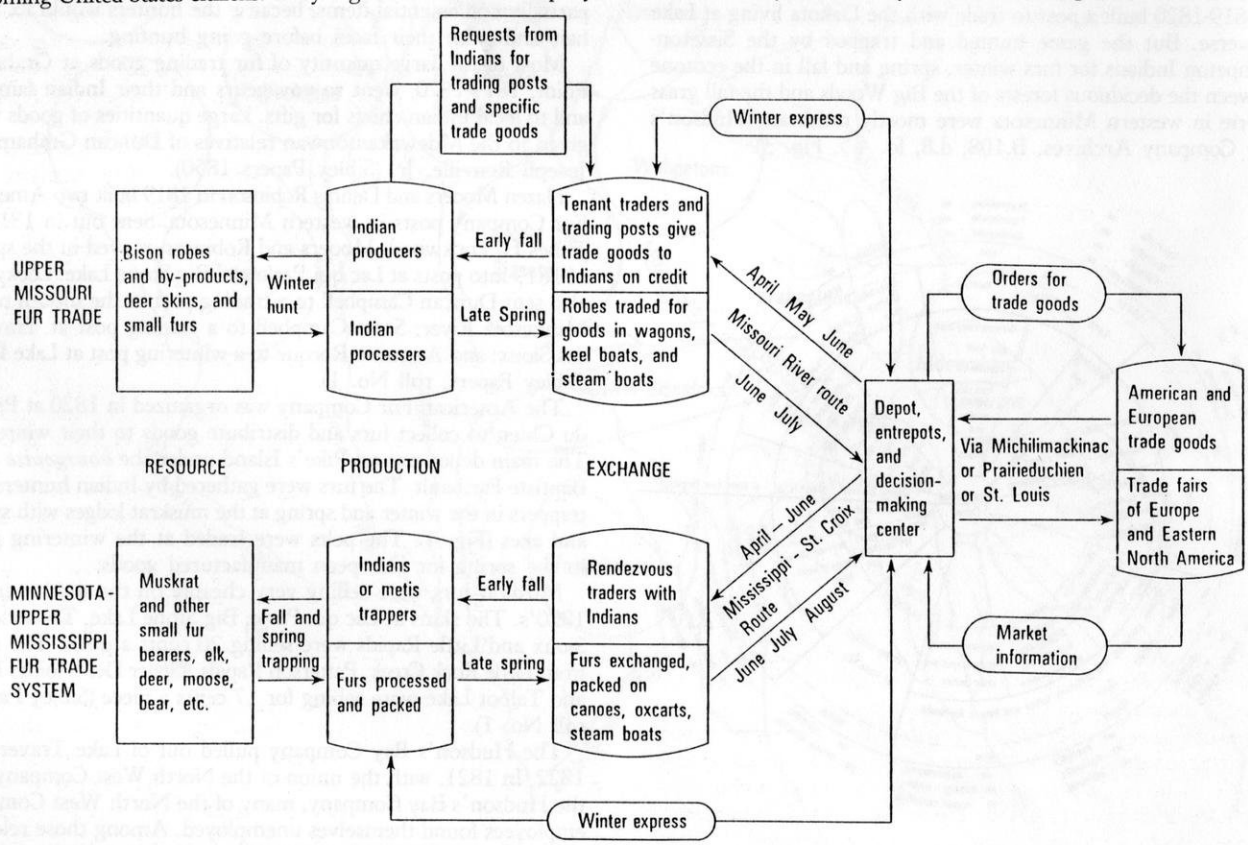

FIG. 5. American fur trade of the Upper Midwest, before 1834: organizational flows.

and then to transport them down to St. Louis (Fig. 5).

Beginning in 1823, steamboats carrying trade goods upstream and furs downstream annually arrived at Land's End for the American fur companies. From Fort Snelling they were carried by water in canoes and keelboats to the eastern edge of the Coteau des Prairies. There they were transported to horses and wagons or oxcarts across the grassy prairies to Indian villages.

Every year the Columbia Fur Company took wagon loads of trade goods to the Oakwood Settlement and exchanged them for robes, pemmican and other furs from the *Oceti Sakowin*. Most of the furs collected consisted of muskrat skins, beaver skins and buffalo robes.

The American Fur Company held onto the muskrat trade and the collections of small animal skins. In the fall of 1826, the price of muskrat furs rose. That fall the American Fur Company sent out a large number of Dakota hunters and trappers armed with iron spears and iron axes into the wet prairies of southern and central Minnesota and along the banks of the Minnesota and Mississippi Rivers for quantities of muskrat hides. But by the fall of 1827, the price of muskrat skins had slumped and John Jacob Astor sold 550,000 muskrat skins for 36 cents a piece and still was left with 200,000 furs he could not sell (Lavendar 1969).

In the fall of 1827, McKenzie, Laidlaw and Lamont were ready to move further west to trade with the three tribes on the Missouri River. The American Fur Company agreed to buy out the posts in Minnesota and as far west as Fort Tecumseh for whatever they were worth. Kenneth McKenzie's inventory of the Traverse des Sioux, Lac qui Parle, Lake Traverse and the fur factory at Land's End amounted to $12,409.75. McKenzie recorded the inventory at Fort Tecumseh to be 4,266 muskrat skins, 1,500 buffalo robes, 850 pounds of beaver pelts, and buildings worth $400.00 to the total of $14,543.00 (Lavendar 1969).

Several years before the inventory was taken by McKenzie at the juncture of the Minnesota and Mississippi Rivers, some of the more enterprising Columbia Fur Company clerks, namely, James H. Lockwood and Alexis Bailly, formed a partnership and bought goods from Joseph Rolette at Prairie du Chien to distribute to their winterers in 1825. They distributed Euro-American manufactured goods to Louis Provencalle at Traverse des Sioux and to Jean Baptiste Faribault at the forks of the Des Moines River (Bailly Papers, Wisconsin State Historical Society). Rolette would supply Bailly and Lockwood with the trade goods on credit in the fall and Bailly and Lockwood would supply Rolette with furs collected in the spring from their Indian hunters and trappers. In 1826, Alexis Faribault traded at Traverse des Sioux for Bailly and Lockwood (Bailly Papers, Wisconsin State Historical Society).

In February of 1828, Alexis Bailly and Joseph Rolette made another agreement, this time only with Alexis Bailly. It specified that Bailly could place anyone he liked at the Little Rapids post including Alexis Faribault. It continued that Faribault could bring the Indians from Traverse des Sioux to trade at Little Rapids if he wanted to. Bailly was to trade only with the Dakota bands at Red Wing's village, Little Crow's village, Black Dog's village, Penishaw's village, Old Sixes (Shakopee) village, Little Rapids village, and with other Wahpetons bands that traded there (Bailly Papers, Minnesota Historical Society). For this privilege Bailly was to pay $666.67 annually to Kenneth McKenzie or 1/3 of the $2,000.00 owed him by the American Fur Company (Bailly Papers, Wisconsin State Historical Society).

By 1829, Alexis Bailly expanded his outfit from Little Rapids to Lake Pepin. Rolette allowed him to trade in August of that year with Red Wing's band, Little Crow's band, Black Dog's band, part of Wabasha's band headed by Old Noyeau, and part of the Wahpekute bands. He could not trade with Black Eagle's band or Blue Spirit bands (Bailly Papers, Wisconsin State Historical Society). Bailly's employees were only to trade within the boundaries of these posts and not outside of them. Their Indians, however, could trap in trapping territories outside of these boundaries.

Bailly's system of trading with the Dakota Indians was on the basis of giving credit to individual persons for goods to hunt and trap muskrats and beavers within their own trapping territory on agreement in writing that the individual Indian would return in the spring with a specified number of furs. If the Indian did not return with the specified number of furs his traps would be taken away from him by the trader.

The Indians never brought in enough pelts to square off their debts. Muskrat furs were the only method of exchange. All of the furs were valued in muskrat skins. At this time, deer skins are valued at two muskrat skins, a raccoon skin was valued at two muskrat skins, and an otter skin was valued at fifteen muskrat skins (Bailly Papers, Minnesota Historical Society).

In 1832, Alexis Bailly and William Brown formed a new outfit to subcontract with Joseph Rolette of the Upper Mississippi Outfit. Their new headquarters were at New Hope, near Fort Snelling. Their trading territory was to be from Traverse des Sioux to the Des Moines River and all points in between Red Wing's village and Lake Pepin. No trading house was to be placed below the mouth of the St. Croix River by Brown and Bailly. Each spring the men and goods of Brown and Bailly's Outfit were to make a voyage to Michilimackinac for the rendezvous there (Bailly Papers, Wisconsin State Historical Society).

Pierre Parrant was hired by Brown and Bailly in 1832 to set up his trading post near Little Crow's village on Frenchmen's Bar near Pig's Eye Lake (Bailly Papers, Wisconsin State Historical Society). Steamboats brought Brown and Bailly's goods to St. Paul from Joseph Rolette at Prairie du Chien (Bailly Papers, Wisconsin State Historical Society).

Brown and Bailly's Outfit in 1833-34 on the Minnesota-Mississippi Rivers were not making much profit. In the winter of 1833-34 Joseph La Framboise, trading on the Cottonwood River with the Southern Sissetons, only produced 300 to 400 maskrat pelts (Bailly Papers, Wisconsin State Historical Society). The Sissetons were only spearing the muskrats in the wet prairies, north and south of the Minnesota River. Joseph R. Brown's trading for Bailly in the winter of 1833-34 at Oliver's Grove, near Hastings, with the Pine Bend band under Medicine Bottle, could only produce packs of smoked or dried rock sturgeon in the spring (Bailly Papers, Wisconsin State Historical Collection). In 1834 Brown and Bailly ended their partnership.

Henry Hastings Sibley arrived in Mendota in the fall of 1834 and bought five wintering posts from Alexis Bailly (Ackermann 1931). These included Mendota, Litter Rapids, Two Woods Lake, the Cannon River and Traverse des Sioux. Bailly's father-in-law, Jean Baptiste Faribault, was wintering at the Little Rapids post; Louis Provencalle was wintering at Two Woods Lake; and Alexander Faribault was wintering at the mouth of the Cannon River (Sibley 1870-80).

Sibley in the winter of 1834, reorganized his posts into the Sioux Outfit of the American Fur Company. In the spring of 1835, he entered into agreements with Joseph Renville, Jr., and Joseph Rolette. The agreement stated that Renville would trade at Lake Traverse and Lac qui Parle for Sibley in return for half of the profits or losses of the posts. The agreement was for five years, but Sibley and Rolette reserved the right to end the arrangements after one year (Ackermann 1931).

Renville's Outfit was to receive trade goods from Sibley to trade with the Indians besides articles for use for himself and his family. He promised only to trade with the Indians who lived within the Lac qui Parle district and not to encroach upon any other outfits of the American Fur Company.

In the summer of 1835, Sibley placed Joseph R. Brown in charge of the stockaded fort at Lake Traverse. Sibley then went to visit Lac qui Parle where the Wahpetons were trading with Renville. Within the stockaded Fort Renville was a dwelling house or store and a magazine. Renville's furs were mostly muskrats, mink, fishers, otters, beavers, raccoons, foxes, badgers, and wolves as well as deerskins, buffalo skins, elkskins, mooseskins and bearskins. A

muskrat skin was worth 16 cents. A gun could be purchased from Renville for 120 muskrat skins or $19.20 for which he paid $6.00 at Mendota. A knife Renville sold to the Dakotas for five muskrat skins or sixty cents. He probably purchased it at Mendota for 20 cents (Willand 1968). By January of 1836, Renville had collected thirty-five packs of muskrat skins to ship down the river to Patterson's Rapids where a barge carried them to Mendota (Sibley Papers 1836).

In May of 1836, the Sheyenne River Outfit of Joseph R. Brown had operated at a loss of $1,000.00. In the spring of 1836, Brown turned over to Sibley, 130 to 135 packs of furs - 80 of which were buffalo robes; 40 of which were muskrat skins; one of which was otter skins; one of which was fisher skins; and the rest of the packs were mixed skins. The Sheyenne River Outfit had only eight packs of spring muskrats and a few packs of otter and beaver skins. The reasons for the poor returns on the Sheyenne River were a lack of ammunition at Fort Renville for the Indians and because of the spreading prairie fires which had been set by Indians (Sibley Papers 1836).

Joseph Renville, Jr., lost $3,000.00 to $4,000.00 worth of muskrat skins that skidded downward in 1837 to five cents a piece. Because of the cheap prices in furs, Renville received an extension of credit to $8,000.00 in 1838. By 1843, when he died, he still owed the company $4,200.00 (Ackermann 1931).

In 1838, William Dickson took the last wagon load of goods to the Oakwood Settlment trading fair which included the Dakotas, Nakotas and Lakotas. In 1839, the Tetons and Nakotas developed their own trading fair in the Black Hills of South Dakota. The Mdewakantonwan, after the treaty of 1837, visited the Indian agent annually at Fort Snelling to receive their goods and annuities. They traded these goods and annuities for liquors which they traded as middlemen to their Wahpetons, Wahpekutes and Sissetons relatives for furs.

CONCLUSIONS

The success or failure of an Euro-American, British or Canadian fur trading company between 1820 and 1838 among the Sisseton-Wahpeton Dakotas were dependent upon the meshing of the strategies of the Euro-American colonial fur trading companies and the local subsistence economies of the local Indian villages. The Sisseton-Wahpeton Dakota Indian fur trade in 1820 was dependent upon the exploitation of the fauna in the natural environment in which they lived and subsisted, whether in the tall grass prairie, the wet prairies, the parkland, or the mixed pine and deciduous forests (Benson 1979). The early fur trading returns from the different companies reflected clearly the ecotones in which they hunted, trapped and collected their food.

Overexploitation of the natural fauna of the region by Dakota hunters and trappers armed with Euro-American manufactured guns, traps, spears and axes, combined with the fall of prices in centralized North American and European markets, greatly restricted the Sisseton-Wahpeton procurement strategies for food, shelter and clothing. By 1835, the Western Wahpetons were down to their last pair of leggings, moccasins and breech clothes, subsisting on wild berries, wild roots, fish and wild fowl (Riggs 1875). Northern Sissetons were hunting the buffalo and digging up *tipsinna* for food on the Coteau des Prairies between the James and Missouri Rivers and trading packs of buffalo meat for corn, beans and squash at the Mandan-Hidatsa and Arikara villages (Will 1950). Eastern Wahpetons were trading small furs for food and goods with the fur traders, missionaries, steamboat passengers and soldiers at Fort Snelling (Pond 1905-08). Southern Sissetons were hunting and trapping for muskrat furs farther and farther into northern Iowa on the Upper Des Moines River and coming into conflict with the Sauks and Foxes over the food resources (Hughes 1905-08).

The Sisseton-Wahpeton procurement strategies were very diverse in 1820, but by 1838 they had become more and more incorporated into the Euro-American colonial economic system. By 1838 the Sisseton-Wahpeton subsistence strategies were restricted, weakening the indigenous trading systems. Once the specialized resources became exhausted, the Dakotas would have few choices for survival in the future:

1. They could live temporarily with their other Siouan relatives;
2. They could live on resources distributed by missionaries, fur traders and governmental agents;
3. They could become impoverished and starve; or
4. They could strengthen the indigenous trading system by partially returning to their annual seasonal subsistence strategies.

After eighteen years of Euro-American economic exploitation, the Sisseton-Wahpetons simply could not go back to all of their 1820 subsistence cycles. By 1838 they were becoming enmeshed for the most part into the Euro-American economic system.

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PHYTOLITH STUDIES AT BIG HIDATSA, NORTH DAKOTA: PRELIMINARY RESULTS

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Abstract. The objective of this study is to evaluate phytolith analysis as a means of reconstructing subsistence patterns at archaeological sites. Phytoliths are microscopic deposits of opaline silica that form in plants, particularly grasses. Subsequent deposition in archaeological sediments preserves evidence of the original plant after all organic remains have decomposed. Several studies have attempted to identify corn phytoliths from early archaeological contexts. Methodology consisted of three steps: examination of modern corn material, comparison to native grasses with similarly shaped phytoliths (identification of characteristic corn phytoliths), and examination of archaeological sediments. Presence of characteristic phytoliths was taken to indicate presence of corn.

To evaluate the accuracy of phytolith analysis a study was conducted at Big Hidatsa, a Plains Village site in North Dakota where corn was a dietary staple. Examination of Mandan corn varieties indicates leaf and husk material produce cross-shaped phytoliths. Preliminary examination of sediments indicates cross phytoliths are rare; distribution is neither abundant nor ubiquitous. Cob chaff yielded short trapezoids, a type abundant in many wild grasses. More research is necessary to characterize corn short trapezoids. Sediment provenience, cultural patterns of plant use and discard, and natural processes must be considered in any interpretation of phytoliths from sediments.

INTRODUCTION

Phytoliths are microscopic mineral deposits that form within and between plant cells. Although the term can refer to any mineral deposit (for example, calcium oxalate crystals in oak leaves), deposits of opaline silica are usually indicated (Rovner 1983). In this paper "phytolith" will refer only to silica deposits.

Three general types of silica deposits have been reported (Sangster and Parry 1981): deposits associated with cell walls, deposits between cells, and deposits that fill cells completely. Families rich in silica include the Gramineae (grasses), Cyperaceae (sedges), Juncaceae (rushes), and Equisetaceae (horsetails).

Several functions have been proposed for phytoliths. Parry and Smithson (1958) proposed that some phytoliths are deposits of excess silica or, alternatively, that silica may act as structural support for plant cells. Kaufman et al. (1981) suggested a function as "windows" to transmit light to inner, photosynthetic tissue. Jones and Handreck (1967) indicated that rice varieties high in silica content are more resistant to fungus attack than those low in silica. Whatever the function, it is known that silica (although not an essential nutrient element) is necessary for the growth of grasses, particularly rice.

Phytoliths are deposited in sediments after decomposition of the organic structure in which they form. Since phytoliths are mineral in nature, preservation often occurs under conditions that can destroy macrobotanical remains. In addition, phytolith analysis can yield data not obtainable from other types of botanical remains. Although many families produce distinctive phytoliths, the most abundant and morphologically varied forms occur in the grass family. Grasses contain specialized cells that accumulate silica, in addition to other cells that may become silicified. Subfamily and tribe may be identifiable by phytolith content, although the task is more complex than it first appeared to be (Twiss et al, 1969, Mulholland and Rapp 1985). Grass pollen grains, on the other hand, all have the same morphology. The only taxon identifiable below the family level is corn, due to larger size. Thus, phytoliths represent a new microfossil with potential applications in paleoecology and paleoethnobotany. However, many variables require further research before phytolith analysis can be used to its full potential.

Phytolith research has been applied to various archaeological and environmental problems. Several studies centered on identification of food plants at archaeological sites. Pearsall (1978) identified corn (or maize) phytoliths at the Real Alto Site in Ecuador. The sediments, associated with hearths, pits, and floors, were dated at 2450 B.C. Piperno (1984) identified corn phytoliths in sediments from several sites in Panama. Two rockshelters, Cueva de los Ladrones and Aguadulce, lacked macrobotanical remains but yielded corn phytoliths from early ceramic contexts. Ladrones also had significant amounts of corn phytoliths in a preceramic context (dated 4910 B.C.). Both Pearsall and Piperno used three general steps. First, native varieties of corn were analyzed for phytolith content. Comparison to native grasses revealed characteristics that distinguished corn from other grass phytoliths. Finally, sediment samples were examined for corn phytoliths; distinctive shapes and/or abundance of shapes was taken as evidence of corn use at that site. In addition, Piperno examined sediments from Sitio Sierra, a late ceramic site where corn cobs and seeds were recovered (Piperno 1984, p. 375). The phytolith assemblage there resembled those from the two rockshelters.

A more extensive test of the accuracy of phytolith analysis is proposed here using samples from Big Hidatsa, North Dakota. Big Hidatsa is a protohistoric/historic Plains Village site located in the Knife River Indian Villages National Historic Site near Stanton. The Hidatsa Indians occupied the site from the 1700's to 1845 (Ahler and Swenson 1985). Corn was a staple food, as recorded by both explorers and ethnographers (Wilson 1917). In addition, corn cobs and kernels were recovered during excavations at the village in 1980 (Ahler, pers. comm.). Therefore, corn phytoliths should be abundant at Big Hidatsa. If absent, the assumptions underlying phytolith analysis must be re-examined.

METHODS AND MATERIALS

Modern plant reference material consisted of native corn plants grown from seed obtained from the Regional Plant Introduction Station at Ames, Iowa. This seed was donated by Oscar Will of Bismarck, North Dakota and is believed to have come from the

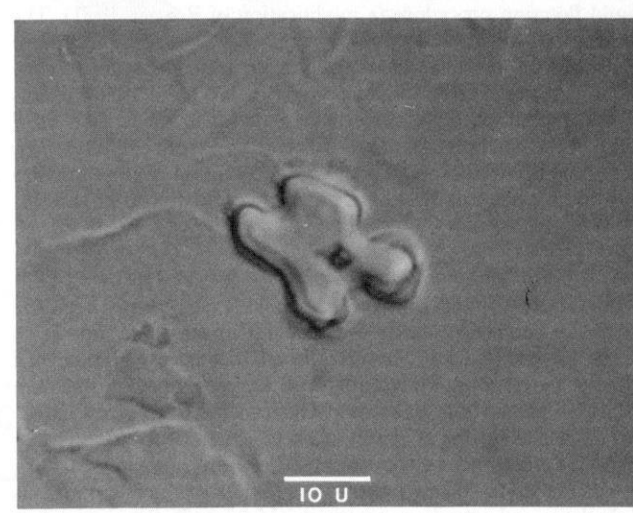

FIG. 1. Cross phytolith from corn (*Zea mays* L.), leaf.

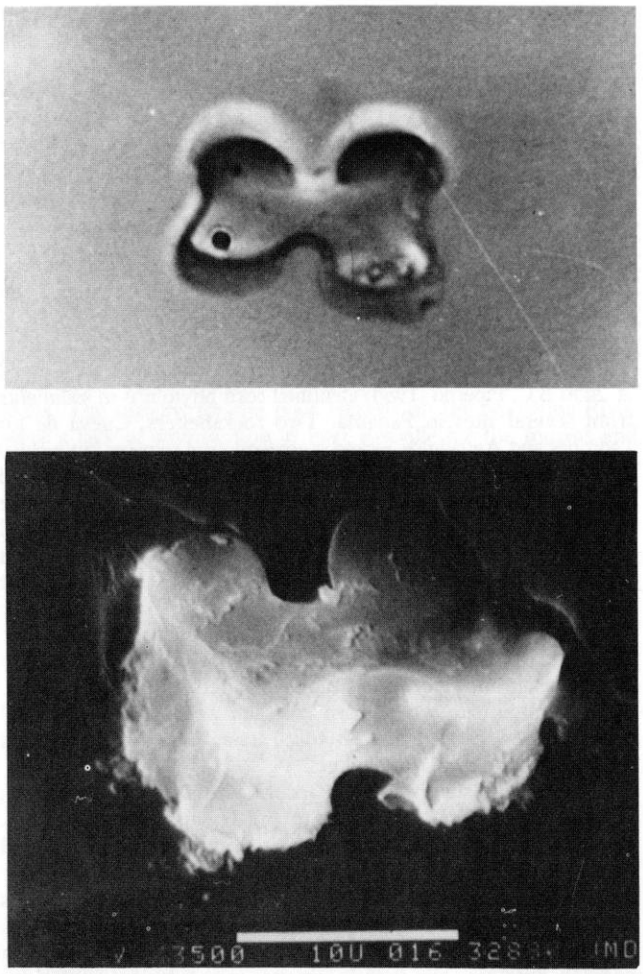

FIG. 2. Dumbbell phytoliths from giant reed (*Arundo donax* L.), leaf.

Mandan Indians. Two varieties, Mandan Clay Red (P.I. 213807) and Mandan Yellow Flour (P.I. 213794), were examined in this initial study. The plants were grown in Duluth, Minnesota. In addition, a collection of wild grasses was made in 1980 from the site area. All plant specimens were digested in a mixture of nitric acid and potassium chlorate (a modification of Rovner 1971, 1972). Sediment samples were collected in 1980 from test pit profiles. Separation of phytoliths was done using a zinc bromide heavy liquid flotation procedure (a modification of Rovner 1971). The preparations were examined using both a Zeiss research microscope equipped for Nomarski differential interference contrast microscopy and a scanning electron microscope (AMR-1000A). Detailed counts of 400 phytoliths each were made at 400x magnification on 7 slides of the corn preparations. All cross and dumbbell phytoliths were measured. Sediment examination consisted of a preliminary scan for crosses followed by a detailed count of 100 phytoliths.

RESULTS

Phytoliths from corn leaves and husks have recently been the subject of detailed research. Pearsall (1978) examined nine races of corn from Ecuador. She established that corn generally had a higher percentage of phytoliths with a cross-shaped outline than did native grasses (Fig. 1 - bar is 10 micrometers in length). ['Cross' was defined as having at least 3 indentations and a length no more than 9.16 micrometers greater than the width.] In addition, corn crosses tended to be larger than those of native grasses. Specimens of the large and extra-large categories (16.03 to 25.19 micrometers on the shorter side) were found only in corn, although these categories represent less than half of the crosses present in most varieties. Later research by Piperno (1984) indicated that some wild grasses (*Oplismenus hirtellus* and a bamboo) do produce large and/or extra-large crosses in quantities similar to corn. However, Piperno determined that corn crosses can be distinguished from those of other grasses by three-dimensional shape morphology. Study of twenty races of corn from Panama showed that corn crosses are mostly symmetrical from top to bottom; that is, both top and bottom are cross-shaped in outline. A few have a rectangle or arch on one side and a cross-shape on the other. Most wild grasses do not produce large quantities of symmetrical crosses. All three factors - percentage of crosses, size categories, and three-dimensional morphology - must be considered when identifying corn phytoliths.

Examination of leaves from two Mandan corn varieties indicated that two of the above factors characterize these varieties. Crosses (Fig. 1) were the dominant phytolith shape observed, followed by dumbbell-shaped phytoliths in much smaller amounts (Fig. 2 illustrates dumbbells from another species). Most of the crosses were symmetrical; both top and bottom faces were cross-shaped. A few possessed a rectangle or arch on one side. Size ranges of the crosses, however, were smaller than those reported for most of the South American varieties. Extra-large crosses were extremely rare (only 2 of more than 700 crosses examined) and large crosses were scarce (46). The vast majority were medium and small in size. Piperno and Pearsall both reported corn varieties with few-to-no large and extra-large crosses, although their research focused on varieties with large crosses. The two Mandan varieties examined thus fit into one end of the range of published phytolith data for corn.

Examination of the grass reference collection indicated dumbbells and crosses are produced by at least some species of all subfamilies represented (Mulholland and Rapp 1985). Before detailed analysis was initiated, selected sediment samples were examined for phytolith content. Sediment samples were chosen from one test unit (Fig. 3) for this preliminary study. The unit, 224 NE 206, is in a midden from the core area of the site. Samples were examined ranging from the top soil layer to a paleosol, including an ash lens and a cache or bell pit. Crosses were very rare, occurring in low quantities in a few samples. Most were small to medium in size. The single exception (Fig. 4) measures 16 1/3 micrometers (21 micrometers in length) and is a large cross. The sample, from a light brown laminar silt containing charcoal, bone, and pottery, is located 15-19 centimeters below the modern soil surface.

It was noted that three samples from the bell pit (Feature 97) had differing amounts of phytoliths. Sample 115, from the center of the pit, had few recognizable grass phytoliths. Phytolith density was low, consisting mostly of nonspecific forms. Sample 116, at greater depth and in a different sediment unit, had frequent grass phytoliths; Sample 117, from the same sediment at the pit base, had abundant grass phytoliths. All three major categories of grass phytoliths (as described in Twiss et al. 1969) were observed in these two samples. Again, crosses were extremely rare and were small or medium in size. Samples 116 and 117 also had nonspecific forms (plant hairs and epidermal cells). If the phytoliths indicate in situ decomposition of plants, the sediment unit at the base of the pit may have had a concentration of grass material. This would confirm one of Wilson's (1917) observations, the lining of bell pits with grass.

DISCUSSION

A goal of many archaeological phytolith studies is identification of plant use at a site. Phytoliths characteristic of corn leaves and husks have been recovered from archaeological sediments, indicating use of corn at those sites (Pearsall 1978, Piperno 1984). This study, designed to check the accuracy of the phytolith record, indicates that not all situations are so straightforward. Although corn was used extensively at Big Hidatsa, characteristic corn phytoliths from

leaves were rare in the sediments. However, sediments from different contexts did contain different amounts and types of phytoliths. It should be possible to relate phytolith assemblages, sediment context, and possible plant use.

The scarcity of cross phytoliths in sediments at Big Hidatsa was disappointing at first. A single large cross cannot be taken as conclusive evidence of corn use at this site, especially since the depth below surface is not great. Although this site was never cultivated (hence no plow zone formed), the possibility cannot be ruled out that this phytolith is a modern contamination from the surface. However, discard patterns of different plant parts may explain this seemingly anomalous situation (Wilson 1917). Corn husking took place in the garden. Most of the husks and all other vegetative material, including leaves, were left there. Phytoliths from these plant parts may therefore help to locate native corn fields. Ears were carried into the village itself, for drying, threshing, and winnowing. Only phytoliths from reproductive material should be expected in any abundance in villages of this period.

Corn kernels, cobs, and chaff were subsequently digested and examined. Phytoliths are not produced by the cob or kernel but are abundant in the chaff. However, chaff phytoliths are not cross-shaped bodies like those found in both leaves and husks. The chaff produces bodies with a circular base and a ridge or rectangular-to-oval raised portion on top (short trapezoids -Fig. 5). Similarly-shaped bodies are abundant in most of the sediments examined. However, this type of phytolith also occurs in many native grasses and much morphological work remains before those from corn can be identified accurately.

This study shows that additional factors must be considered as part of any phytolith study. Cultural patterns of plant use and

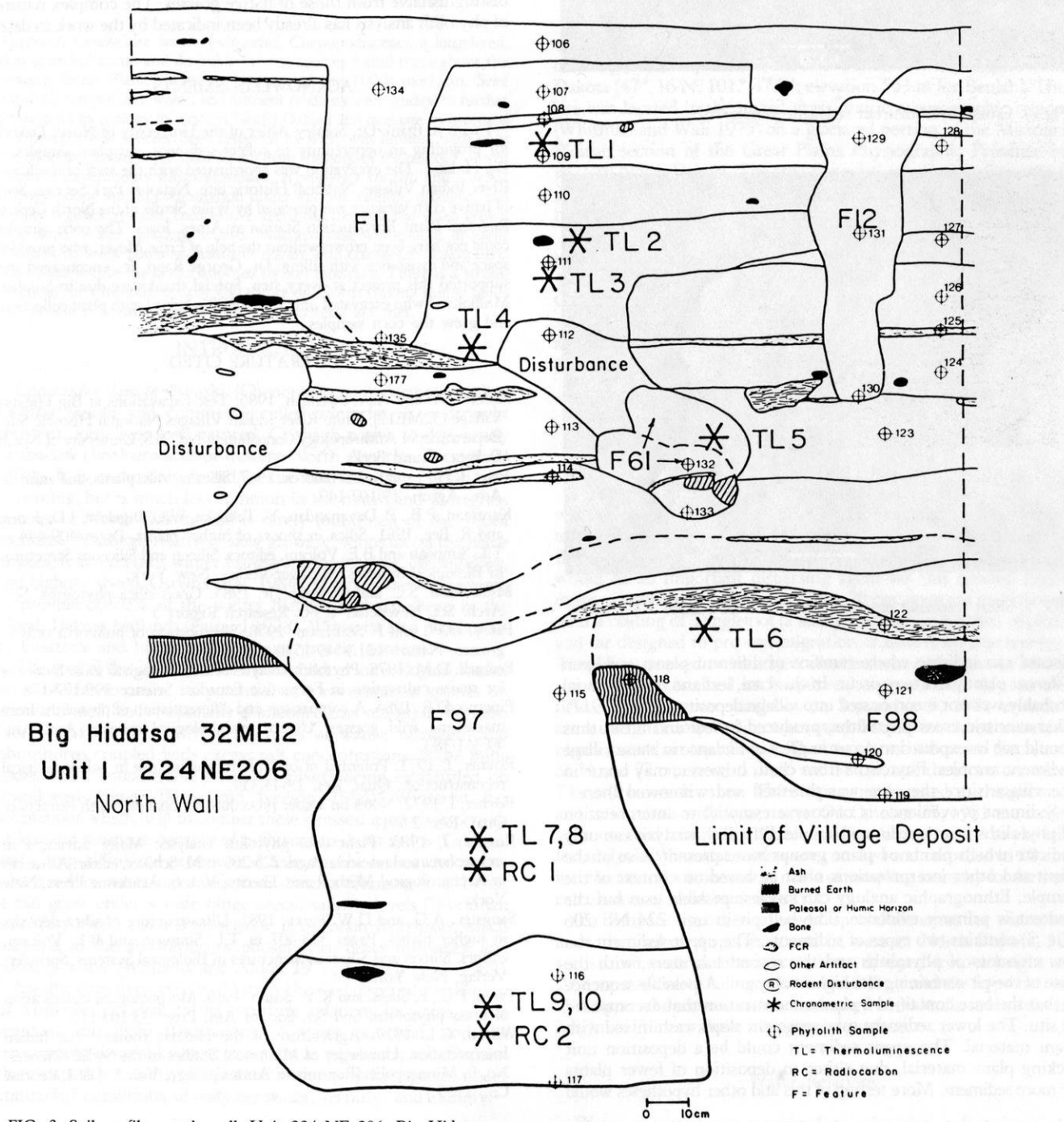

FIG. 3. Soil profile, north wall, Unit 224 NE 206, Big Hidatsa.

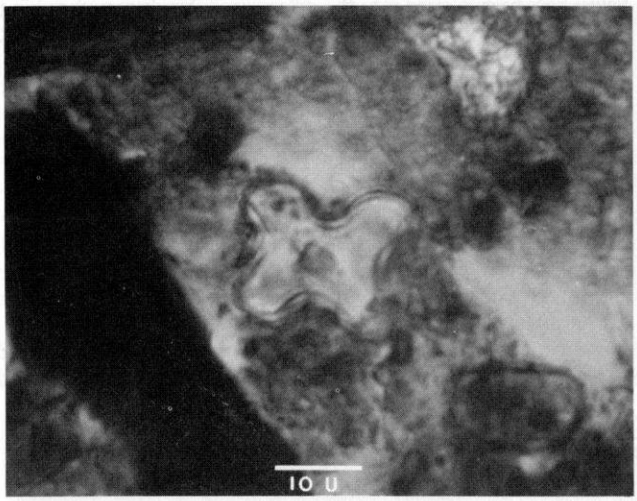

Fig. 4. Cross phytolith from sediment sample 107.

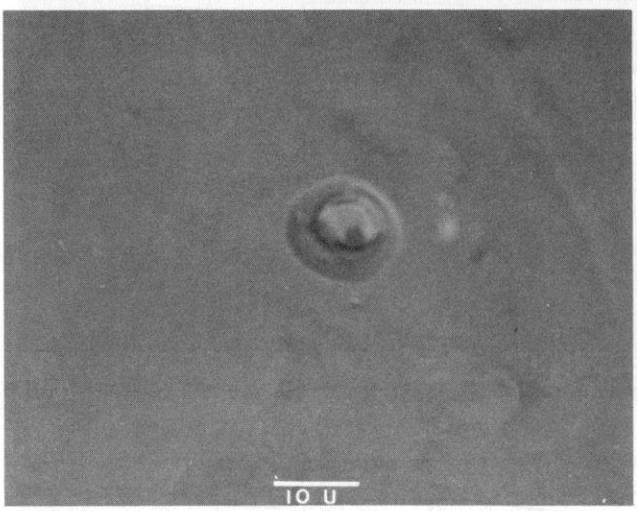

FIG. 5. Short trapezoid phytolith from corn (*Zea mays* L.), chaff.

discard can indicate where remains of different plants and even different plant parts may occur. In this case, leaf and husk material probably was not incorporated into village deposits (Wilson 1917). Characteristic cross phytoliths, produced in leaf and husk, thus should not be expected to occur in great abundance in these village sediment samples. Phytoliths from chaff, however, may occur in the village since the corn was threshed and winnowed there.

Sediment provenience is of course essential to interpretation of phytoliths from a sediment sample. Phytolith analysis can only indicate which plants or plant groups were present. Use of the plant and other interpretations must be based on context of the sample. Ethnographic analogy can suggest possible uses but the context is primary evidence. The bell pit in unit 224 NE 206 (Fig. 3) contains two types of sediments. The upper sediment has low amounts of phytoliths and the second has more, with the base of the pit containing the highest amount. A possible sequence is that the base contained a plant concentration that decomposed in situ. The lower sediment may represent slope wash mixed with plant material. The upper sediment could be a deposition unit lacking plant material, due either to deposition of fewer plants or more sediment. More testing of this and other hypotheses would include careful comparison of artifact content and microstratigraphy of the two levels.

Other factors should also be considered. Post-depositional sediment processes may affect phytoliths. Sampling and laboratory procedures must be checked to eliminate bias in the samples. The characteristics that distinguish corn phytoliths from those of other grasses must be tested, until all grasses have been examined, to establish the degree to which corn is distinct. Modern sediments must also be examined to determine the natural "background" phytolith deposition. Comparison of cultural sediments to modern A horizons should show differences due to cultural activity.

Phytolith analysis is not a simple procedure nor are most variables understood to a sufficient degree. Much basic research needs to be done. In this study, the next step is clear - short trapezoids must be examined in detail to see if those from corn chaff are distinguishable from those of native grasses. The complex nature of phytolith analysis has already been indicated by the work to date.

ACKNOWLEDGEMENTS

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Part 2. PRAIRIE PLANTS AND PLANT COMMUNITIES

COMPETITIVE, SEED DISPERSAL, AND WATER RELATIONSHIPS OF WINTERFAT (*Ceratoides lanata*) IN WESTERN NORTH DAKOTA

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Abstract. Ceratoides lanata (winterfat, Chenopodiaceae), a long-lived, slow-growing shrub and desirable browse species found throughout the western Great Plains, is infrequent east of the 100th meridian. Seed dispersal, competition, water, and nutrient relations were studied to further understand its ecology in western North Dakota and evaluate its potential as a revegetation species. Seed dispersal by wind was limited, with only 4% of seeds moving more than 50 cm from the edge of the plants. Growth chamber experiments with *Ceratoides*, *Agropyron smithii* and *Kochia scoparia* alone and in combination under various salinity, drought, and fertility regimes, revealed competitive inferiority for winterfat when grown from seed. Water relations studies indicated that winterfat is drought resistant; its water potential fluctuates readily with changes in atmospheric conditions within the limits imposed by soil moisture. There is a strong potential for winterfat to exist and thrive on North Dakota mined lands and prairie restorations if establishment criteria are met.

INTRODUCTION

Ceratoides lanata Neuski (Chenopodiaceae), formerly called *Eurotia lanata* and commonly called winterfat, is a drought resistant, long-lived low statured, C_3 shrub native to dry, sandy or shallow clay loam soils of western North America (Springfield 1974). It is commonly found in the cold deserts of Utah and Wyoming, but is much less common in the mixed and shortgrass prairies of North Dakota and is rarely found east of the 100th meridian. Although relatively slow growing, winterfat (as the name implies) is an excellent winter browse species for deer, elk, antelope, and bighorn sheep (Ostyina et al. 1984). In fact, it has been shown to provide 60-70% of the winter diet for bighorn sheep in the North Dakota badlands (Fairaizl 1978). Winterfat also is palatable to livestock and high in energy and protein content.

The goal of this investigation was to conduct autecological studies on winterfat to assess its potential as a revegetation species on surface mined lands (especially abandoned coal mines) in Western North Dakota. Typically, deficiencies of water, nitrogen, and phosphorus coupled with excess salt concentrations in the mine spoils cause considerable stress for plants being established on abandoned mines (Bares and Iverson 1984). Winterfat has adaptations which help to combat these stresses: it survives periods of low soil moisture because of high root-to-shoot ratios (Caldwell and Camp 1974) and pronounced hairs on the leaves and stems, which reduce water vapor loss from stomata (Branson et al. 1976); it can grow under a wide range of soil salinity levels (Workman and West 1969); and it is reported to have endomycorrhizae, which may aid in the absorption of phosphorus, other nutrients, and possibly water (Williams and Aldon 1976; Lindsey et al. 1984).

Specific objectives were to (1) study the seed dispersal mechanism of winterfat; (2) evaluate its moisture relations in terms of the seasonal and daily fluctuations of water potential, and the environmental variables most important as regulators; and (3) assess the competitive ability of winterfat with two other species under controlled conditions of varying water, fertility, and salinity.

STUDY AREA

The seed dispersal and water relations studies were conducted on a large relatively undisturbed area 4-5 km NW of Beulah, North Dakota (47° 16′N, 101° 47′W; elevation 543 m for Beulah). The site was located in the mixed grass prairie ecogeographic region (Whitman and Wali 1975) on a glaciated portion of the Missouri Plateau section of the Great Plains Physiographic Province in western North Dakota. The area was relatively good quality mixed grass prairie and had not been grazed intensively but had been hayed occasionally in recent years.

The area has a semi-arid, continental climate with an annual mean precipitation of 440 mm, (74% of which falls during the 120-day growing season) and a mean annual temperature of 4.7° C (July mean of 22° C, January mean of -13° C). In 1981, the year of this study, the climate was slightly warmer (5.9° C mean annual temperature) and drier (392 mm precipitation) than normal (National Oceanic and Atmospheric Administration 1981).

METHODS

Seed Dispersal

A method was designed to assess the pattern and amount of winterfat seed dispersal by wind. Since the fruit is a one-seeded utricle consisting of a nutlet enclosed in two bracts, each bearing fluffy white hairs (Springfield 1974), it seemed likely that wind would be an important dispersing agent for this species. Eight strips of polyethylene sheeting, 300 x 20 cm, were cut and painted with a coating of Tanglefoot (a sticky commercial product of pitch and tar designed to prevent migration of insects up tree trunks). Tanglefoot proved to be an excellent substance for use in sticky traps, as it maintained its 'stickiness' even after 52 days in the field. The strips were laid out on September 5, 1981 as radial arms in eight compass directions away from two isolated winterfat plants located on top of a hill. The two plants had crown diameters of 74 and 77 cm, heights of 36 and 38 cm, and their centers were 75 cm from each other. The strips were fastened to the ground at 1-m intervals with wire stakes. On October 27, 1981 the strips were covered with cellophane, rolled up, and returned to the lab for analysis. Winterfat seeds were counted and recorded in 10-cm increments; calculations were made of sampling intensity for further calculation of seed rain density.

To compare hypothetical seed dispersal distances for winterfat and other selected species found in western North Dakota, 12 seeds from each of nine species were dropped from a height of 2.67 m to calculate falling velocities in still air and the hypothetical seed dispersal distances with a wind speed of 30 km/hr and a release height of 30 cm above the ground surface.

Water Relations

Water potential was measured on winterfat at four intervals during 1981: June 7-9, July 28-29, August 8-9, and September

TABLE 1. Wind dispersal of winterfat seeds trapped on sticky traps.

Distance (cm)	Sampling Intensity (% area)	# Seeds	Corrected Seed Rain (seeds/m^2)	% of Total	Cumulative %
0-10	21.7	32	740	23	23
10-20	20.0	26	650	21	44
20-30	18.5	27	930	23	67
30-40	17.3	17	490	16	83
40-50	16.2	11	340	11	94
50-60	15.2	3	100	3	97
60-70	14.3	1	40	1	98
70-80	13.6	1	40	1	99
80-90	12.9	1	40	1	100
90-100	12.3	0	0	0	100
100-300	8.1	0	0	0	100
Total		119		100	

4-5. Stems of the current year's growth and of similar diameter (2-3 mm) were selected from five plants and were measured for water potential by the pressure bomb technique (Scholander et al. 1965), using a PMS Model 2000 pressure bomb (PMS Instrument Co., Corvallis, Oregon). Plants were monitored at each sampling date approximately every 2 hours for a minimum of 30 consecutive hours. In addition to measuring water potential, several environmental variables were monitored for correlation with water potential. Air temperature and relative humidity were recorded with a Weather Measure hygrothermograph, while light intensity and duration were monitored with a Belfort recording pyrheliograph. Soil temperatures were measured with thermistors at depths of 0.5, 5.0, 10.0, 20.0, and 40.0 cm. Wind speed was recorded at a nearby weather station (4 km away at Montana-Dakota Utilities' Coyote Power Station). Vapor pressure deficits were calculated by using tables of water vapor pressure (as related to relative humidity) against temperature. These variables were then included in multiple regression analysis to determine their relative importance in fluctuating water potentials. Factors affecting seasonal water potential fluctuations were also assessed over the 1981 season. Twenty-four hour means of air temperature, relative humidity, vapor pressure deficit, solar radiation, wind speed, and soil temperatures at 0.5, 5.0, 10.0, 20.0, and 40.0 cm were compared to mean water potentials over the four sampling dates. In addition, soil water variables (% water and pF in soil at depths of 0-5, 5-10, 10-15, and 15-20 cm), precipitation variables (precipitation during the previous 1, 2, 3, and 4 weeks), and air temperature variables (temperature means for the previous day and previous week) were included in the analysis. Soil water was determined from soil samples representing the various depth intervals and were analyzed for water content gravimetrically. The pF of the soil was determined for by the filter paper method (McQueen and Miller 1968). Precipitation and air temperature for the presampling days were obtained from the Beulah NOAA weather station (4 km from the study sites).

Growth Chamber Experiment

A growth chamber experiment was designed to determine the influence of varying amounts of soil water, fertility, and salinity on the growth of *C. lanata* (winterfat), *Kochia scoparia* (kochia), and *Agropyron smithii* (western wheatgrass) individually and in combination with one another. Eight soil treatments were established: two levels of water irrigation (30% and 60% of field capacity maintained daily) x two levels of fertilizer (no fertilizer and 150 ppm N, 100 ppm P and 50 ppm K added) x two levels of salinity (no salt and 0.5% NaCl added). Seeds of the three species were sown in sand and were allowed to germinate before being transplanted into 11 cm pots. Four plants were transplanted into each pot - four plants of each species planted in monoculture and mixed combinations of two plants each of kochia with winterfat and winterfat with western wheatgrass. There were eight soil treatments x five species combinations x three replicates for a total of 120 pots in this experiment. Plants were grown in a growth chamber under the following conditions: 25° C day and 15° C night temperatures, 16 hours of daylight, 25-50% humidity, and roughly 150 microeinsteins per m^2 per second of photosynthetically active radiation (PAR). After 54 days, plant shoots were harvested, oven dried to constant weight at 65° C, and weighed.

RESULTS AND DISCUSSION

Seed Dispersal

A total of 119 winterfat seeds were captured on the 20 x 300 cm sticky traps. Of the seeds, 67% were trapped within 30 cm of the plants, and only 6% travelled more than 50 cm away. No seeds were trapped farther than 90 cm from the plants (Table 1). Assuming that no seeds blew farther than 3 m and that all seeds were dispersed from the plants during the September 5 to October 26 period, the total number of seeds dispersed by the two plants was calculated to be 702 seeds, or about 350 seeds per plant. These data indicate that winterfat is not a good candidate for rapid colonization of mined areas by wind dispersal mechanisms, although Woodmansee and Potter (1971) used circumstantial evidence to estimate seed dispersal at up to 250 m in New Mexico.

There was a strong correlation between wind characteristics and seed dispersal (Table 2). Wind directions, through estimates of wind duration (hours in October 1981 in which the wind blew from a given direction), average wind speed, and especially wind force (duration x average windspeed), were highly correlated with the direction in which seeds were dispersed.

The fruits of winterfat averaged 2.94 mg in weight, fell from 2.7 m at an average velocity of 147 cm/sec, and had an expected dispersal distance of 170 cm when at a height of 30 cm with the wind blowing at 30 km/hr (Table 3). Winterfat seed weight is relatively high compared with those of seeds of most other local colonizing species accounting for the short dispersal distances found in the field even though winterfat fruit bracts are profusely hairy. Those species with estimated dispersal distances greater than that of winterfat (*Lepidium densiflorum*, *Bouteloua gracilis*, and *Aristida longiseta*) also have various structures on their fruits which increase air resistance and reduce falling velocities. Those species with seemingly no fruit structures adapted for wind dispersal (i.e., *Kochia scoparia* and *Agropyron caninum*) have the lowest estimated dispersal distances (Table 3). However, kochia has another method of wind dispersal in its 'tumbleweed' nature, which makes it an excellent disperser across the prairies (Iverson and Wali 1982).

TABLE 2. Duration, average wind speed, and total force of wind from each compass direction for the period October 1-26, 1981, and the number of winterfat seeds trapped (wind data furnished by the Montana-Dakota Utilities Co.).

Direction	Duration (hrs.	Avg. Wind Speed (km/hr)	Total Wind (km of wind)	# Seeds
N	73	23.2	1691	29
NE	35	11.0	384	0
E	123	18.9	2321	24
SE	113	22.2	2507	12
S	168	31.2	5236	48
SW	23	19.9	457	1
W	31	15.9	491	2
NW	58	19.3	1119	3
Correlation with number of seeds:	r= 0.867 (P<0.01)	0.838 (P<0.01)	0.960 (P<0.001)	

TABLE 3. Seed weight, falling velocity in still air, and estimated distance of dispersal under hypothetical conditions of 30 km/hr wind speed and 30 cm seed height for winterfat and eight other western North Dakota species.

	Seed Weight (mg)	Velocity (cm/sec)	Distance Dispersed (cm)
Lepidium densiflorum	0.27	120 a[1]	209
Bouteloua gracilis	0.29	122 a	205
Aristida longiseta	2.02	130 ab	192
Ceratoides lanata	2.94	147 bc	170
Andropogon scorparius	1.73	164 cd	153
Artemesia frigida	0.05	178 cd	140
Ratibida columnifera	0.52	196 d	127
Kochia scoparia	0.61	278 e	90
Agropyron canium	37.58	293 e	85

[1] Numbers followed by similar letters are not different at the 0.05 level of significance using Duncan's test.

Water Relations

Water potential was measured in 350 winterfat twigs during 70 sampling times over the four sampling dates in 1981. Water potential extremes were -0.17 Megapascals (MPa) at 0600 hrs on a humid, cool June morning to -5.55 MPa at 1600 hrs on a hot, windy, dry September afternoon. Maximum daily fluctuation for any single 24-hour period on a single plant was -5.55 MPa at 1600 hrs September 4 (relative humidity 41.5%, soil temperature at 1 cm 31.7° C, air temperature 23.1° C, wind speed 41.4 km/hr) to -0.55 MPa at 0800 hrs the next morning (relative humidity 100%, soil temperature at 1 cm 16.1° C, air temperature 14.7° C, wind speed 9.7 km/hr, light rain). This indicates a considerable capacity of the species to adjust its water potential to accommodate prevailing conditions.

In daily fluctuations of water potential values, significant correlations existed between water potential and vapor pressure deficit, air temperature, soil temperature at 1 cm, and relative humidity, in decreasing order. Vapor pressure deficit was most important, with correlation coefficients of 0.90, 0.98, 0.96, and 0.86 for June, July, August, and September sampling dates, respectively. When all variables were entered in the equation for all sample points, the R^2 value was 0.90 ($P<0.0001$).

Six of 25 measured environmental variables were significantly correlated with seasonal fluctuation of water potential (mean values for five 24-hr periods) (Table 4). Again, vapor pressure deficit had the highest correlation, but surface soil water was also important. The highest water potentials were recorded when the soil and air were dry and the temperatures were high.

The water potential of the air (vapor pressure deficit) appears to be the primary factor regulating water potential in winterfat plants, but the water potential of the soil is important in determining the level to which vapor pressure deficit can regulate water potential in the plant. Under dry soil conditions (for example, the September sampling date), all plant water potentials had greater negative values than when soil moisture levels were adequate (June), even though vapor deficit values were equivalent.

These results generally confirm those by other workers. Love and West (1972), working in Utah, found seasonal fluctuations of winterfat water potential largely due to variations in soil moisture. Their range in water potential was about -8.5 MPa when soil moisture was 2.7% in mid-July to -1.8 MPa when soil moisture was 10.2% in late August 1968. Ruess and Wali (1980) also found that diel fluctuations of water potential in *Atriplex canescens* (four-wing saltbush) were controlled largely by vapor pressure deficit. Poole and Miller (1975) found diurnal fluctuations to be greater when soils were moist than during dry periods. The study of Pavlik (1980) and this study, however, found the greatest diurnal fluctuations when soils were driest.

Indications are that winterfat is very drought tolerant. In this North Dakota study, the species had good vigor at plant water potentials below -5 MPa, and it has been reported to have potentials as low as -10.5 MPa in Utah (Love and West 1972) and -9 MPa in Colorado (Branson et al. 1976). This capacity to withstand low soil moisture is a tremendous asset for surviving in mined land ecosystems.

TABLE 4. Environmental variables correlated with water potential over five 24-hr periods.

Factor	
Vapor pressure deficit	0.981
Soil water, 0-5 cm	-0.947
Relative humidity	-0.877
Soil temperature, 1 cm	0.862
Solar radiation	-0.850
Soil temperature, 40 cm	-0.847

TABLE 5. The effect of water, fertilizer, and salinity treatments in combination with each other on the growth of four plants of monocultures of winterfat, kochia, and western wheatgrass.

	Dry Matter Yield (g/pot)		
MAIN EFFECTS	Winterfat	Kochia	Western wheatgrass
+ Water	0.55	2.04	1.18
- Water	0.38	1.34	0.53
+ Fertilizer	0.72	2.86[1]	1.41[2]
- Fertilizer	0.21	0.52[1]	0.30[2]
+ Salt	0.02[1]	1.70	0.13[1]
- Salt	0.91[1]	1.68	1.57[1]
Overall mean	0.47	1.69	0.85
INTERACTIVE EFFECTS (L = low level, H = high level)			
$Salt_L$ $Water_L$ $Fert_L$	0.42 c[3]	0.50 f	0.41 de
$Salt_L$ $Water_L$ $Fert_H$	1.06 b	2.70 c	1.60 c
$Salt_L$ $Water_H$ $Fert_L$	0.37 c	0.39 f	0.63 d
$Salt_L$ $Water_H$ $Fert_H$	1.80 a	3.11 b	3.65 a
$Salt_H$ $Water_L$ $Fert_L$	0.02 d	0.45 f	0.02 f
$Salt_H$ $Water_L$ $Fert_H$	0.13 d	1.71 d	0.08 ef
$Salt_H$ $Water_H$ $Fert_L$	0.41 d	0.72 c	0.12 ef
$Salt_H$ $Water_H$ $Fert_H$	0.09 d	3.92 a	3.05 b

[1] Significant at P<0.001
[2] Significant at P<0.05
[3] Numbers within a column followed by similar letters do not differ significantly at the 0.05 level using Duncan's test.

Growth Chamber Experiment

Treatment effects on pure stand growth. Winterfat and western wheatgrass had maximum production in the high moisture, high fertilizer, and low salt treatment, but kochia did best under high salinity (Table 5). This finding demonstrates the halophytic properties of kochia (Monk and Weibe 1961, Iverson and Wali 1982). Winterfat did not grow well on the high salt treatment (0.5% NaCl), as the seedlings often died. It has been reported that winterfat does not establish well under saline conditions (Workman and West 1969, Goodman 1973), and the present results seem to substantiate those claims. However, winterfat plants were observed to survive (although not vigorously grow) in North Dakota field plots with levels of salinity equivalent to those in this experiment.

Kochia had nearly twice the production of western wheatgrass and nearly four times the production of winterfat (Table 5). Winterfat and western wheatgrass exhibited highly significant decreases due to salinity, but kochia was slightly stimulated by salt (when water was sufficient). Kochia and western wheatgrass also showed a significant response to fertilizer over the entire experiment (Table 5).

For all species, the adding of fertilizer caused significant effects on growth and indicated the desirability of fertilizing during the revegetation process. The simulated drought caused the greatest relative decline in the yield of western wheatgrass (a reduction to 45% of the high-water yield, compared with 66% for kochia and 68% for winterfat). Western wheatgrass, a cool season C_3 grass, apparently needs more water per unit of dry matter production than do the other two species. The capacity to tolerate drought stress had previously been documented for kochia (Iverson and Wali 1982) and winterfat (Caldwell and Camp 1974) and is supported by this study.

Competitive relations. This experiment was designed as a 'replacement series' after de Wit (1960) and Harper (1977). The replacement series consisted of a total of four plants/pot in this manner: (1) species A alone (four plants); (2) species A (two plants) growing with species B (two plants); and (3) species B alone (four plants). The yields in pure stands vs. mixtures were then analyzed to assess competitive relations between the species pairs (Figs. 1 and 2). Eight treatments (combinations of salt, fertilizer, and moisture) and three species (winterfat, kochia, and western wheatgrass) were used in the experiment.

The results of experiments based on the replacement series can take any of four basic forms (Harper 1977):

1. Model I - Equivalent demands by each species on environmental resources. The growth of two species in mixture results in each contributing to the total yield in direct proportion to its representation in the sown seed. This can happen in two ways: either the density is so low that there is no interference, or the effect of A on B is precisely the same as that of B on B and the effect of B on A is the same as that of A on A. This model was not found to hold in this experiment although Fig. 2a (winterfat vs. western wheatgrass at low water, low fertilizer, low salt) is close to fitting the model (the two species yield lines should intersect midway across the x axis, and the total yield line should be straight and horizontal).
2. Model II - Differential demands by each species on environmental resources. This is the most commonly reported situation; two species are making demands on the same resources, but there is some difference in resource use between them. This model is exemplified in this experiment by Figs. 1c, 2e, 2f, 2g, and 2h. In Models I and II, the yield in mixtures is predictable from the yields in pure stands in that a straight line connecting the pure stand yields will intersect the sum of the mixed yields (the total yield line across the top of the figures is a straight line connecting the pure stand yields). Contrary to Model I, however, the intersection of the species yield lines is not midway across the x axis. The intersection of the two yield lines gives some indication of the competitive nature between the two species (i.e., competitive

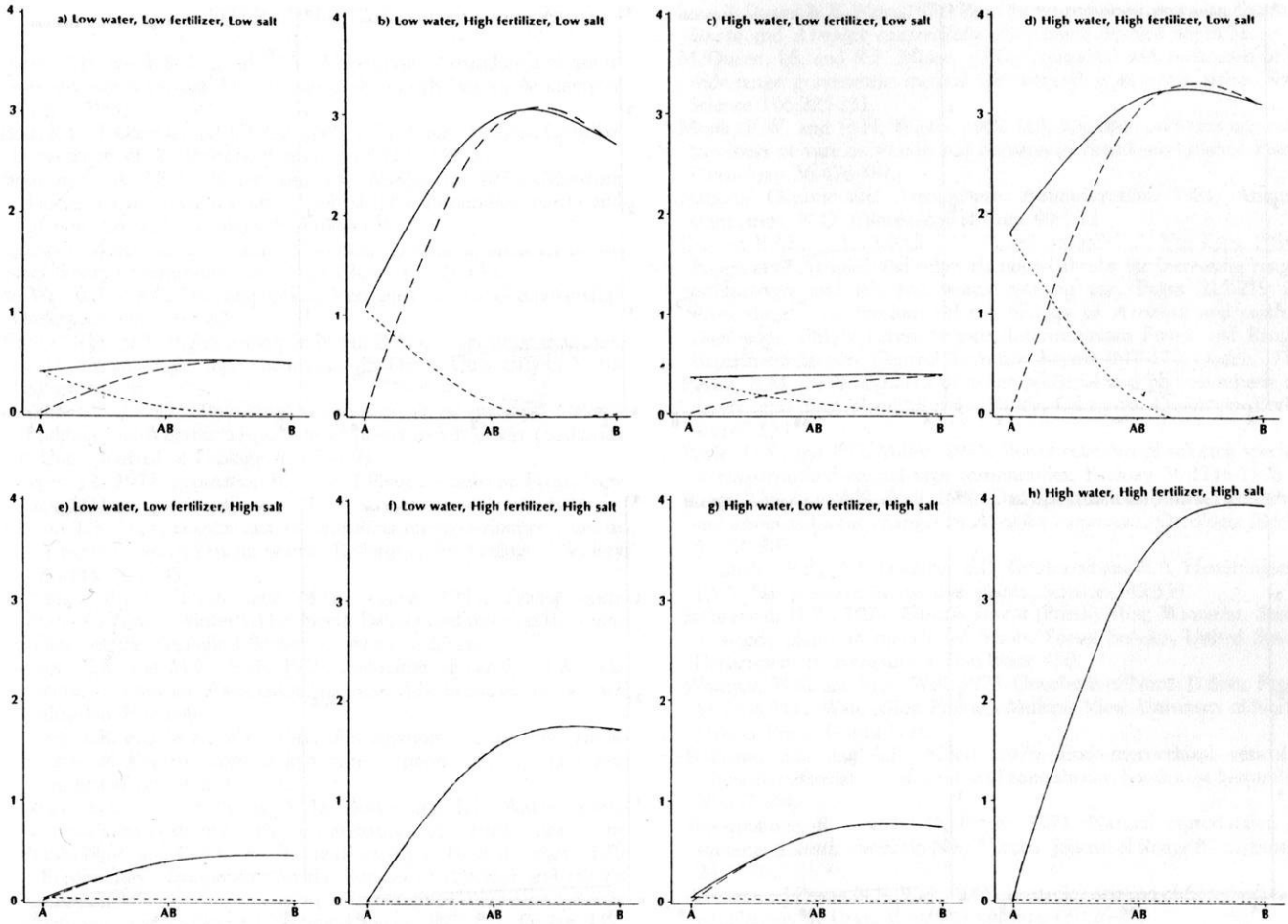

FIG. 1. Yield results (in grams per pot on the Y axis) of replacement series between kochia (species A - long dashed line) and winterfat (species B - short dashed line), with the species mixture noted AB. Total pot yields are marked by solid lines for eight combinations of water, fertilizer, and salt levels.

superiority is inferred for kochia in Fig. 1c, since the intersection lies to the left of center).

3. Model III - Mutual antagonism. In this case, the effect of A on B is greater than that of B on B and the effect of B on A is greater than that of A on A. Neither species contributes its expected share in mixed stands, and the total yield line is concave in appearance. This model would fit if each species damaged the environment of the other more than it damaged its own environment (i.e., allelopathy). Model III was not found in this experiment.

4. Model IV - Mutual benefits. Each species fails to suffer as much as expected from the presence of the other, and the total yield line is convex in appearance. Some method of avoiding competition occurs. This model was fitted by experiments illustrated by Figs. 1a and 1b.

In all eight treatments of the kochia-winterfat species combinations, kochia exhibited higher yields (with inferred competitive superiority) than winterfat (Figs. 1a-1h). However, in the case of high salinity, it can be assumed that little competition occurred, since winterfat growth was extremely small. This superiority is expressed graphically in the figures in that the species yield lines always intersect to the left of midpoint (Model II). Winterfat fared relatively better against kochia when water was high and fertilizer and salinity were low (Fig. 1c). It appears that the two species compete for the same resources under most situations and that the rapid growth characteristic of kochia also means a relatively greater demand for resources. Results of the winterfat-western wheatgrass species combinations again indicate competitive inferiority of winterfat in nearly all treatments, though the magnitude of the differences were smaller than with kochia (Figs. 2a-2h).

At first glance, the results seem confusing until one considers the life history strategies of the three species. Kochia, known to be a fugitive, ruderal species, was competitively superior to western wheatgrass and winterfat, and winterfat was competitively inferior to each of the others. Kochia is a very fast-growing, annual, halophytic, drought tolerant chenopod, which excels on North Dakota mined (disturbed) areas for the first 2 years, only to be completely eliminated 4 years after mining (Iverson and Wali 1979, 1982). Winterfat, on the other hand, though also a member of the Chenopodiaceae, is a very slow-growing species, and it may take 70 years to reach a height of 60-90 cm in Utah salt deserts (Goodman 1973). Winterfat is a drought-tolerant, long-lived perennial species which grows well when the areas are not too saline and there is not too much grazing. Western wheatgrass is a fast-growing, perennial, cool-season grass which is drought tolerant as well as alkali tolerant (Best et al. 1971).

The rate of initial growth can be critical to the outcome of competition among seedlings in small containers. The rapid shoot growth of kochia may have given rise to shading effects, and its rapid root growth may have depleted nutrient and water resources that would otherwise have been available to other species. In the field, the rapid growth of kochia makes it be an excellent "nurse" crop (it protects seedlings from excessive drying and wind damage) and can initially be beneficial for the establishment of grasses (Iverson and Wali 1982) and winterfat (Woodmansee and Potter 1971). After a few seasons of growth, kochia most likely would

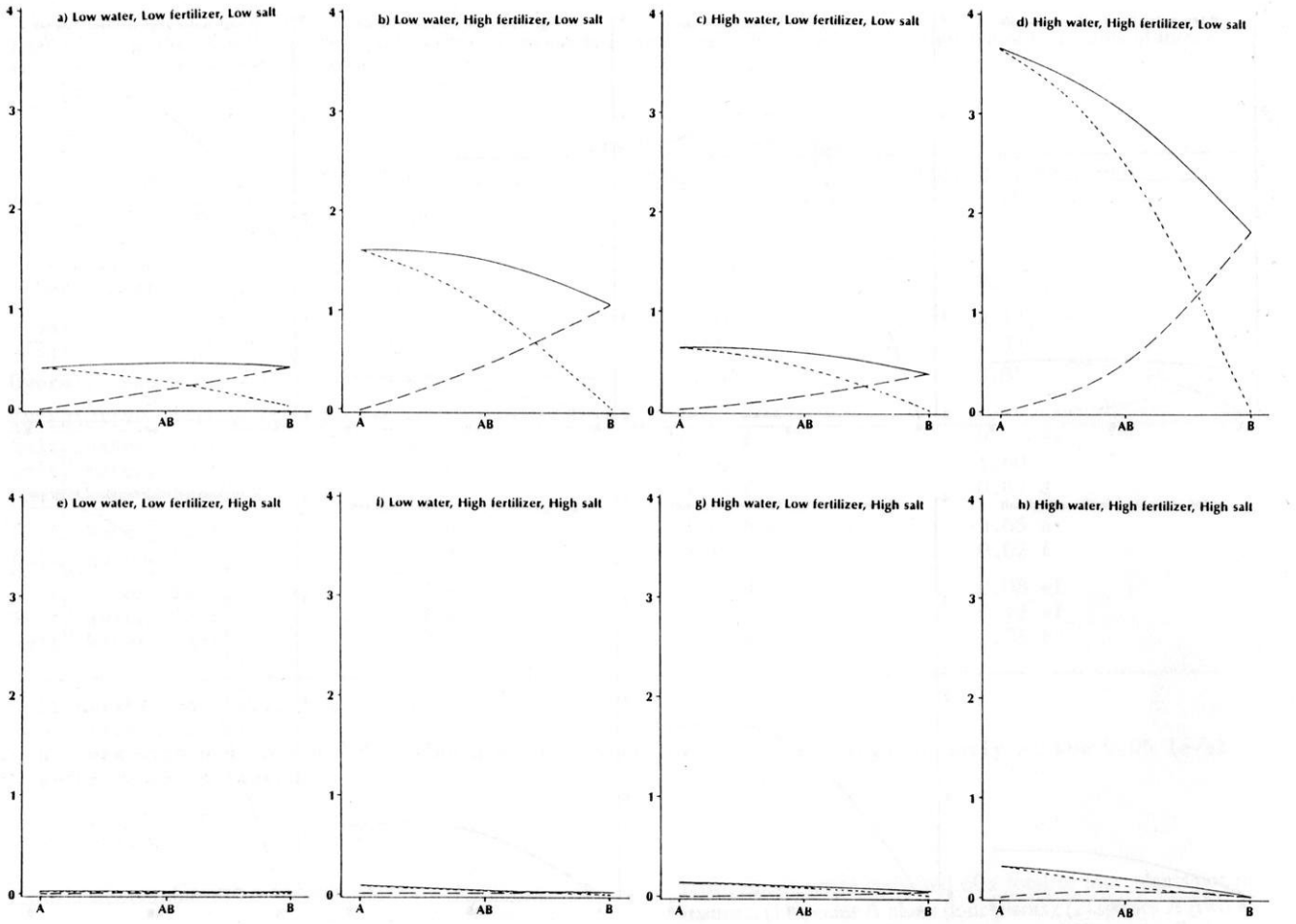

FIG. 2. Yield results (in grams per pot on the Y axis) of replacement series between winterfat (species A - long dashed line) and western wheatgrass (species B - short dashed line), with the species mixture noted AB. Total pot yields are marked by solid lines for eight combinations of water, fertilizer, and salt levels.

lose its competitive advantage unless the area is extremely saline, as it has to start from seed each year, whereas the other species can continue to grow from their perennating organs. Under extremely harsh conditions (Iverson 1983), kochia can survive for extended periods but would be subject to interspecific competition and autotoxicity (Iverson and Wali 1982). Winterfat and western wheatgrass probably can exist on a site long after kochia is replaced.

Given the difficulties in establishing winterfat from seed, another potential method for establishing winterfat on harsh sites is by transplanting containerized seedlings. A growth chamber experiment developed to test transplanting success of seedlings established in favorable soil into harsh soil media (high salinity, low water, low nutrition) showed winterfat to have 100% survival using this method (Iverson et al. 1984).

CONCLUSIONS

Winterfat, though having fruits with hairy bracts, is not well adapted to natural dispersion by wind in North Dakota. The majority of the seeds are dispersed less than 50 cm from the plant in the direction of the predominating winds.

Winterfat is highly drought resistant. Its water potential responds readily and primarily to changes in the atmospheric water potential, although soil moisture is critical in setting the limits in which atmospheric demands change the water potential in the species.

When growing from seed, winterfat is apparently competitively inferior to western wheatgrass and especially inferior to kochia under the conditions of soil moisture, soil fertility, and soil salinity used in this study. After establishment, however, it is believed that the long-lived nature of winterfat would slowly move the competitive balance in favor of winterfat.

The autecology of winterfat needs to be explored further, but it has good potential as a desirable reclamation species. It grows well on disturbed habitats for establishment, is drought tolerant and moderately salinity tolerant, and is long-lived providing the area is not overgrazed. The species is highly desirable as a browse species and would enhance the often low plant diversity of reclaimed areas. However, the species may need a 'nurse' crop for establishment (kochia is a prospective ''nurse'' crop on newly mined areas) and must not be grazed for the first few years to gain proper establishment. Transplanting winterfat seedlings on harsh sites (like abandoned mine lands) is recommended.

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THE PHENOLOGY AND POLLINATION BIOLOGY OF *ANEMONE PATENS* (RANUNCULACEAE) IN WESTERN MINNESOTA

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Abstract. The pasqueflower, *Anemone patens*, occurs in northern temperate grasslands. During April and May in the prairies of western Minnesota, a flower blooms for seven to nine days and fruits for an average of 23 days. The flower stalk grows below the flower's bract when the plant is in bloom and above the bract while the fruit is maturing, keeping the head above the surrounding vegetation. The flower may be pollinated by a variety of insects, particularly flies, and bees in the genus *Andrena* whose primary nectar and pollen source is *Salix*. In the rigorous, early spring climate insect activity may be limited so that outcrossing may not take place although insect exclusion tests showed that pollination can still occur. This species of anemone is adapted to such conditions with an additional self pollination mechanism.

INTRODUCTION

Pollinators of prairie plants are poorly understood and rarely recorded because virgin prairies are scarce and because support for studies of native prairie forbs is limited. Recent interest in prairie restoration has generated questions about the natural components of prairies, special adaptations and the interrelationships of the plants and animals that together constitute a prairie ecosystem.

One of the earliest plants to appear and flower in the tallgrass prairies of the upper midwestern United States and Canada is the pasqueflower, prairie crocus or mayflower, *Anemone patens* L., (= *Pulsatilla patens* (L.) Mill.). This is a primarily northern perennial species that persists in virgin prairie and disturbed prairie situations including old fields, cemeteries, hillsides and open woods which have encroached onto old prairie habitats (Wildeman and Steeves 1982, Uotila 1969, Lundquist 1977). It is tolerant of mild disturbances such as fires, grazing and mowing but not major disruptions such as digging and plowing.

Anemone patens is distributed in North America from Alaska through the prairie provinces of Canada, east to Michigan and Illinois, and south to Oklahoma and Texas in suitable unplowed areas wherever tallgrass prairie has existed. Its old world distribution in Scandinavia, western Europe, and the Soviet Union is described by Lundquist (1977), Uotila (1969), Zimmermann and Meihlich-Vogel (1962), and Kalliola and Kalliola (1935). In spite of its broad distribution, little is known about the species, its pollinators or pollination biology. Population studies in Finland have been published by Uotila (1969). A preliminary account of its phenology is given by Wildeman and Steeves (1982) in a paper on the

developmental morphology of this species in Canada, and Barth (1985) mentions that the flower is proterogynous, its stigmas becoming receptive before the anthers mature.

The generic nomenclature for this species is discussed by Ennis (1973) and by Wildeman and Steeves (1982). In this paper I follow their generic designation, "*Anemone*," for this species rather than "*Pulsatilla*," the name preferred by European writers.

The buds and meristem tissue of *Anemone* lie at or just below the surface of the ground and start to grow soon after the snow melts (Wildeman and Steeves 1982). It is the earliest flower to bloom in the upper midwest and thus is subjected to sudden and severe changes in temperature and weather conditions. Thus, it is of interest to understand how this species and its potential pollinators are adapted to such rigorous climatic conditions.

The purpose of this study was to obtain information on the phenology of *Anemone patens*, to understand its pollination biology, and to determine its potential pollinators. Knowledge of pollination mechanisms contributes to the data base from which their evolution can be understood. Information on the natural plant-animal relationships of virgin or undisturbed native prairie is also of value when evaluating the effectiveness of prairie restoration projects.

MATERIALS AND METHODS

Field work took place from April 14 to June 12, 1984, on the 15 ha (37 acre) Strandness Prairie, 4 miles NE of Starbuck, Pope County, in west-central Minnesota. The prairie which is owned and managed by the Minnesota Chapter of The Nature Conservancy, has never been plowed or grazed but has been maintained by either mowing or, in recent years, by biannual burning.

To study the phenology of *A. patens*, 38 buds that were about to open and showed purple petals through the bracts were marked with a flag and a numbered metal tag. The length of the lower stalk at this stage was measured from ground surface to the base of the bract. Measurements were taken two to three times a week throughout the growing period. As the flower grew, the length of the flower stalk both below and above the bract was recorded and correlated with the stage of development of the plant.

To understand the pollination biology, 44 other buds were covered with fine mesh "bridle veil" nylon netting bags which were fastened tightly around the flower stalk below the bud to exclude potential pollinators. U-shaped wire braces held the netting above and away from the flower when it opened. Each bud was numbered, flagged and allowed to develop naturally to determine whether or not seed set would take place when pollinators were excluded.

Pollen and nectar collecting visitors were observed and periodically collected throughout the prairie but not from flagged plants. Collections were made on *Salix*, the only other flowering species on the prairie at the start of the study. Voucher specimens of visitor species are located in the prairie insect collection at the University of Minnesota, Morris.

PHENOLOGY AND GROWTH PATTERNS

The growth rate of the flower stalk during each stage of development is plotted in Fig. 1. Each stage and its duration is described in Table 1.

Buds

Flower buds emerge from the ground in central Minnesota shortly after the snow melts at the end of March or early April. In 1984, flowering started during the first week in April and continued on this prairie through the first week in June. When buds first emerge they are covered by hairy, fingerlike bracts. As the bud swells the purple petals show through the bract (Stage A).

TABLE 1. Phenological stages in *Anemone patens*: Description and duration.

Stage	Description	Days in Stage
A	Bud stage; measurements started when bud showed purple through the bracts	1-5
B	Flower open; no pollen	1-7
C	Flower wide open; stemens spread; pollen present	1-6
D	Corolla closing, all pollen shed	1-5
E	Corolla closed, drying, brown, separating from base	2-9
F	Petals gone, fruit starting to develop	2-6
G	Fruit developed on full head	2-15
H	Fruit dry and dispersing until gone	6-8
I	Fruit gone, stalk stands until withered	7-

Flowers

In the early part of the season, flowers took longer to develop than those later in the season. The flower opens during the day and closes at night. When the bud first opens, the multiple stigmas are spread over the top of the immature anthers (Stage B). Just before the pollen is shed, the stigmas become erect and contiguous, the stamen filaments elongate and the anthers spread. Anther dehiscence takes place two to eight days after the bud starts to open ($n = 20$, $\bar{x} = 4.0$, $SD = 2.1$) (Stage C). If pollination has not occurred by the time the anthers dehisce, the stigmas again spread over the top of the anthers. They straighten again if pollination takes place. In seven to nine days after the bud opens ($n = 7$, $\bar{x} = 7.3$, $SD = 0.7$) the flower remains closed (Stage D), the pistils turn red and the anthers start to wither. The petals turn brown and soon drop off (Stage E).

Fruiting

While the petals are being shed, the styles elongate and their short hairs fluff out. If pollination has occurred the fruit head spreads to form a dandilion-like cluster (Stage G). If pollination has not taken place, the flower parts cease growing and wither with no further seed development, the flower stalk dries and the head drops off. Stigmas that receive pollen continue to develop so that some heads contain both withered and developed fruit. Fruit development from the dropping of petals to shedding of fruit (Stage H), takes an average of 8 days ($n = 14$, range = 7-21, $SD = 3.6$). The whole developmental cycle from mature bud to shedding of seed averages 38.5 days ($n = 7$, range = 30-46, $SD = 6.5$).

Leaves

Leaves start to appear after the plant has finished flowering. They dry up in July but persist frequently into the next growing season (Wildeman and Steeves 1982).

Growth Rate

The bud starts to open when the flower stalk below the bract averages 60 mm long ($n = 10$, range = 51-68, $SD = 5.3$). As the flower opens it is supported by the bracts and is thus protected at its base where the nectaries are located. Growth takes place by elongation of the flower stalk below the bract. Growth continues below the bract until the petals wither and start to shed. The stalk length below the bract grows to an average height of 89 mm ($n = 38$, range = 55-170 mm, $SD = 22.4$). Elongation above the bract starts when pollen is shed with an average growth rate

of 30 mm in three to seven days (Fig. 1). When the flower starts to wither the length of the stalk above the bract increases rapidly until the fruiting head is fully grown, attaining an average of 150 mm (n = 214, range = 70-230, SD = 28.8) in 23 days. Thus, the length of the stalk above the bract may become half again as long as that below the bract (Fig. 1). This growth rate keeps most flowers and fruiting heads above the sprouting grasses and emerging vegetation.

POLLINATORS

The only published record of insect visitors on *Anemone patens* is *Andrena* (*Parandrena*) *andrenoides* which visits *Anemone patens* for nectar (Krombein et al. 1979), its primary pollen source being *Salix*. Visitors taken during this study are listed in Table 2. They were primarily feeding on nectar. All bee species were occasional visitors and none appeared to be either obligatory or regular pollinators of *Anemone patens* at this study site. The most frequent bees were andrenids and one species of *Colletes*. They collected pollen primarily from the two species of *Salix* that grew on the prairie and occasionally visited the *Anemone* to feed on both the pollen and nectar. The only pollen collecting bee seen on *Anemone* was *Andrena sigmundi*. This species collected pollen late in the season after *Salix* had finished blooming. Flies, primarily muscoids, anthomyids and tachinids, were more numerous than bees throughout the flowering period of the *Anemone*. Mirid bugs (Hemiptera) were most numerous the last two weeks of April. Coleoptera were prevalent from the end of April to mid May. Thrips were active in the flowers throughout the flowering period and also occurred in the bagged plants. No other insects were seen in bagged flowers.

The prairie harvester ant *Formica obscuripes* also fed on nectar of *Anemone*. All these groups are able to contribute to the pollination of the plant. Thrips, however, were not seen with pollen, their bodies being only slightly larger than a pollen grain. The most active visitors were the bees, flies and mirids which readily flew from plant to plant. In searching for nectar, insects landed on the petals and crawled to the base where the nectary was located. Some crawled over the stigmas to get to the other side. If pollen was present in the flower, nectar feeders became covered with the pollen. Since both the pollen and stigmas were sticky, pollen transfer took place whenever stigmas were contacted.

POLLINATOR EXCLUSION RESULTS

Flowers that were bagged in the bud stage effectively excluded all insects except thrips. Of the 44 bagged plants, 37 developed to the fruiting stage (the rest were blown away, broken or otherwise destroyed). Of these, 60% set seed, contrasting with 82% of non-bagged, monitored plants. Although these differences are statistically significant by the Student's T-test, future comparisons should also be made with larger populations of undisturbed flowers since collecting or measurement activities could have affected pollination in the test samples. However, the large percentage of plants that set seed in bagged flowers suggests that some mechanism is operating other than insect pollination.

Seed Germination

Attempts were made to germinate both the mature and the apparently undeveloped seed but no germination was achieved.

Weather Conditions

During this study, the wind was particularly strong, gusting on several days to 25 to 35 mph. Many of the early flowers became battered before fruiting took place. Some plants that had bloomed early in the season produced new flowers during May. Such growth from dormant buds is discussed by Wildeman and Steeves (1982) and is an adaptation to early blooming conditions in boreal habitats.

TABLE 2. Insect visitors to *Anemone patens*.

HYMENOPTERA
Apoidea (Bees)
Andrenidae
Andrena carlini
Andrena erithrogaster
Andrena mariae
Andrena sigmundi
Andrena nigra
Andrena miserablis
Andrena imitatrix
Andrena (Micandrena) sp.
Andrena sp.
Colletidae
Coletes sp.
Halictidae
Halictus sp.
Lasioglossum sp.
Anthophoridae
Ceratina sp.
Epeoplus sp.
Apidae
Apis melifera
Other families:
Formicidae
Formica obscuripes
Tenthredinidae

HEMIPTERA
Miridae
Scutellaridae

HOMOPTERA
Fulgoridae

COLEOPTERA

DIPTERA

THYSANOPTERA

DISCUSSION

Anemone patens is well adapted morphologically to growing and developing under harsh climatic and environmental conditions (Wildeman and Steeves 1982). Although no specific pollinator species can be identified, the plant does attract a variety of insects to its nectar. Bees, flies, beetles and other insect visitors can effect pollination but do not seem to be needed for the plant to set seed since seeds were produced when all insects except thrips were excluded. Thus, pollination must take place either by the thrips or through some other mechanism. In this study thrips were not considered to be effective in pollination because of their small size and limited mobility between plants. However, in future studies, their exclusion should be attempted.

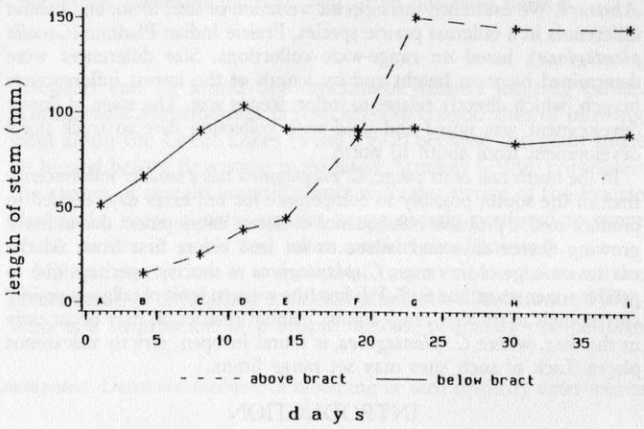

FIG. 1. The growth rate of the flower stem of *Anemone patens*. The points on the graph represent each stage in the development of the plant as indicated by the letters at the bottom of the graph. The average length of the stem above and below the flower bract is plotted for each stage against the average number of days in each stage.

Stage: A = mature bud; B = open flower before pollen is shed; C = flower with shedding pollen; D = corolla closing; E = petals shedding; F = fruit starting; G = fruit fully developed; H = fruit dry, dispersing; I = all fruit dispersed from drying stalk.

During April and May of 1984, winds commonly gusted 30 to 35 mph. Although wind pollination of *Anemone patens* may be possible, it is unlikely since the pollen is large and sticky and not easily blown out of the flower. Self fertilization is also possible. When pollen is released by the anthers, the upper flower stalk starts to grow and the flower is no longer supported by the bract. It readily nods in the wind. Flowers close at night and remain closed if the weather is cold or overcast and windy. Since unpollinated stigmas spread above the anthers, they are likely to contact pollen when the flower head is blown about in the wind. This could also occur in the bagged flowers and could explain the high percentage of those flowers that set seed. Since some heads did not develop seed in both bagged and unbagged plants, it seems unlikely that apomictic mechanisms are involved.

Cross pollination does occur when insects visit plants for nectar. This ensures some outbreeding. But the growth and developmental strategies of *A. patens* also contribute to its pollination if outcrossing fails. Thus, in an uncertain climate in which insect activity may be limited by cold or inclement weather, *Anemone patens* seems well adapted to set seed by more than one pollination mechanism.

ACKNOWLEDGEMENTS

The Nature Conservancy is gratefully acknowledged for permitting this research on their preserve. I also thank Dr. Wallace LaBerge for the identifications of *Andrena*, and Andy Lopez and particularly Laura Smith for their help with the graphics.

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COMPARISON OF MORPHOLOGICAL CHARACTERS BETWEEN REGIONAL HABITATS OF CACALIA PLANTAGINEA (ASTERACEAE)

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Abstract. We examined intraspecific variation of size, form, and habitat differences in a tallgrass prairie species, Prairie Indian Plantain (*Cacalia plantaginea*), based on range-wide collections. Size differences were determined by stem height and by length of the lowest inflorescence branch, which directly relates to inflorescence size. The stage of flower development was noted and used with collection date to track floral development from south to north.

In the north half of its range, *C. plantaginea* has a smaller inflorescence than in the south, possibly to compensate for ten extra days needed to produce seed, a probable consequence of slower development due to fewer growing degree days and failure to set seed before first frost. At the northwest edge of its range, *C. plantaginea* is shortest, perhaps due to greater water stress: the 60% P:E line (the western limit of tallgrass prairie) corresponds to its west range limits. Habitat restriction may occur only in the east, where *C. plantaginea* is found in open, strictly calcareous places. Lack of such sites may set range limits.

INTRODUCTION

This study is an investigation of intraspecific variation of size, form, and habitat differences in a tallgrass prairie species, Prairie Indian Plantain (*Cacalia plantaginea*), among different segments of the species range, with special attention to the species border.

Since the early 1900's, with the work of Griggs (1914), Transeau (1903) and others, species have been thought to have distinctive appearances, behaviors, and/or habitat restrictions (Bantock and Price 1975) at the geographical edges of their range (which we call the species border). Daubenmire (1978) distilled the possible causes of these phenomena into three elements: genetic change (speciation); habitat restriction; and alteration of form and function (dwarfism, lack of seed set, etc.). Reduction in size and restrictions of local populations and individuals may be the result of physiological stress (Shumaker and Babble 1980). With the development of electrophoresis and other techniques, there has been renewed interest in the species border, especially from an evolutionary and genetic standpoint (Levin and Clay 1984).

The question of range-edge species bahavior is complex, since elements overlap and interact, sometimes synergistically. Niering et al. (1963), for instance, found that interaction of physical (temperature and altitude) and biological (disease) factors in the saguaro cactus at the edge of its range caused a decline in density, but no range contraction. Range contraction eventually might occur because there are fewer adults as ''nurse'' sites for seedlings.

Genetic change (foreshadowing speciation) is assumed to be most likely at the species border because there the species is at the limits of its ecological tolerance. Local range-edge populations are more susceptible to detrimental effects of disease, predation, competition, and inclement weather (Hartl 1980). Thus environmental selection pressures should be strongest at range edge.

Reduction in size, flowering, seed set and germination in individuals of a species can be range-edge phenomena (Daubenmire 1978, Griggs 1914). The direct cause of these phenomena is often

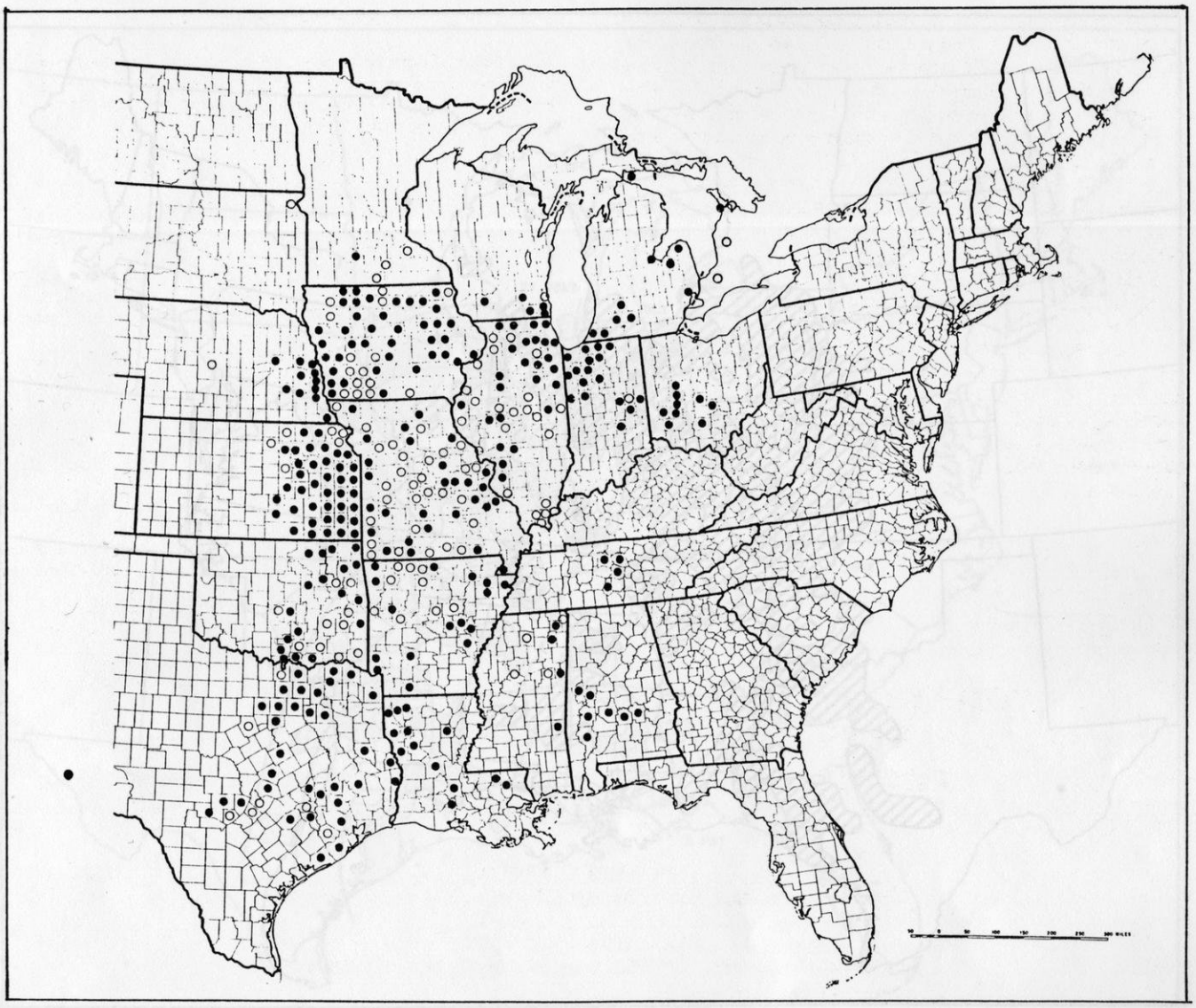

FIG. 1. Distribution of *Cacalia plantaginea* by county. Data collected from herbarium specimens indicated by ●, from published floras ○.

attributed to climate, chiefly temperature and precipitation if edaphic factors are not involved. These phenomena reduce competitive ability and, if persistent at a site over years, extirpation can occur. Populations at the species border also ought to experience greater losses in natural catastrophes and be eliminated from sites more easily than populations toward the center of the range.

Edaphic factors are also responsible for population reduction or isolation of populations. McLean (1970) documented that populations of serpentine-dwelling plants are separated from others because of intervening expanses of non-serpentine soils. Other instances can be found of non-climatic factors limiting range. *Ammophila breviligulata* is restricted to coastal sites of blowing sand along the Great Lakes (Voss 1972) because the plant must be buried before flowering is initiated. Stuckey (1983) correlated the ranges of certain aquatic plants with the wedge of the Prairie Peninsula, these aquatic species being mostly confined to more acidic waters of pools and lakes outside the Peninsula.

Habitat restriction in a species at range edge is taken as the consequence of diminished ecological amplitude (Daubenmire 1978). This is a summation of multiple factors, primarily competition

TABLE 1. Days required between full bloom and seed maturity in *Cacalia plantaginea*. Dates are medians of blooming or seed maturity dates within each zone. Number of specimens are in parentheses.

Zone	Range of days in blooming period		Date of full bloom	Date of seed maturity	Days needed to maturity
I	4/24-5/8	14	5/5 (5)		
II	5/9-5/28	19	5/18, 5/19 (10)	6/12 (5)	24-25
III	5/29-6/17	19	6/7, 6/8 (22)	6/29, 6/30 (6)	21-23
IV	6/18-7/7	19	6/29 (45)	8/2, 8/3 (22)	34.35
V	7/8-7/27	19	7/14, 7/15 (18)	8/17 (6)	33-34
VI	7/27-8/10	14	8/5 (5)		

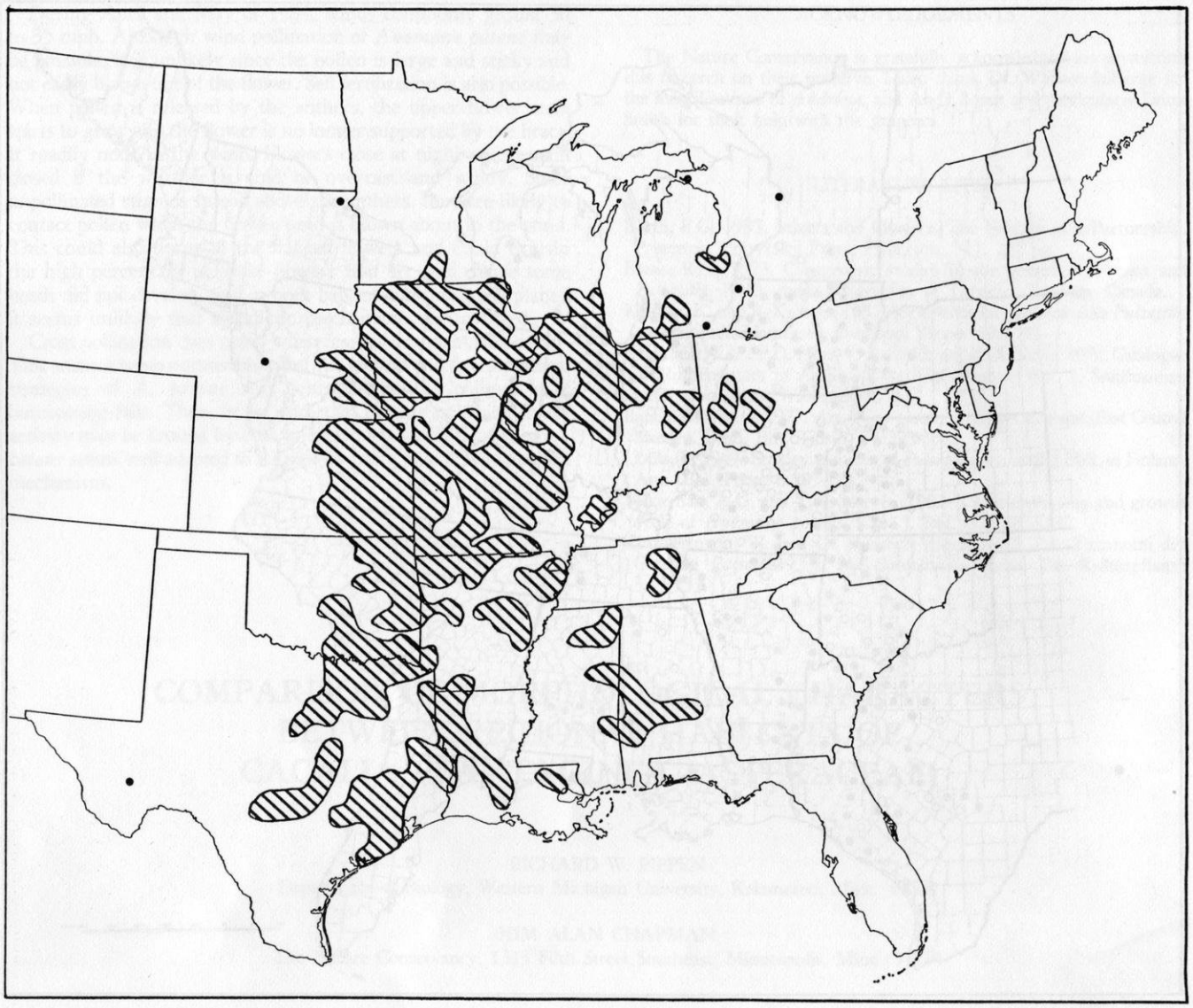

FIG. 2. Range map of *Cacalia plantaginea* distribution. Outlying single collection indicated by ● A cluster of dots separated from another by a line of counties was considered a single unit of range.

from species adapted to prevailing conditions and absent from the rest of a species' range, and lessened vigor due to extreme conditions. Habitat restriction can be expressed in dominance shifts across narrow microclimatic lines. At high altitudes in the Rockies, for example, Daubenmire (1943) found oak-pine forest on south slopes and spruce-fir on north.

The notion that species occupy "favorable" and specific habitats at the species border because of microclimatic factors was questioned by Griggs (1914), who reasoned that, because many plant species he examined at the respective species borders had large and vigorous populations, though local and rare, the climate must be suitable for them. But microclimate and its effects on species must be considered. A species at its range-edge may exist only in habitats of favorable microclimate because it is generally out-competed elsewhere by species better adapted to the prevailing conditions. Favoring this argument are relict species of dry, exposed habitats (e.g., bedrock outcrops, steep southerly hillsides) which flourish when planted in richer sites nearby. In Michigan some of such species (Marquis and Voss 1981) are cordilleran disjuncts (e.g., *Chamaerhodos nuttallii*, *Arabis holboellii*, *Arenaria macrophylla*, *Collinsia parviflora*) and their occurrence in Michigan is readily attributed to lessened competition at these more sparsely vegetated places.

Distance between populations and individuals can itself restrict gene flow, especially if species border populations are disjunct from the main population. This may result in character differentiation, which can be unique in different regions of a species' range (Daubenmire 1978). Phenotypic variation in species is considered a consequence of plastic responses of individuals to factors in the environment (Davis and Heywood 1963). Environmentally malleable morphological traits include leaf shape, stem height, and time of flowering, which are well-known to become fixed in local populations, termed "ecotypes" (Bidwell 1979).

METHODS

Data Collection

Data for this study were collected from 727 herbarium specimens of *Cacalia plantaginea* from 26 herbaria (see acknowledgements for list of herbaria). Location, habitat information, phenological condition and date of collection were taken from specimen labels and supplemented from 11 published floras (Barkley 1977, Branner

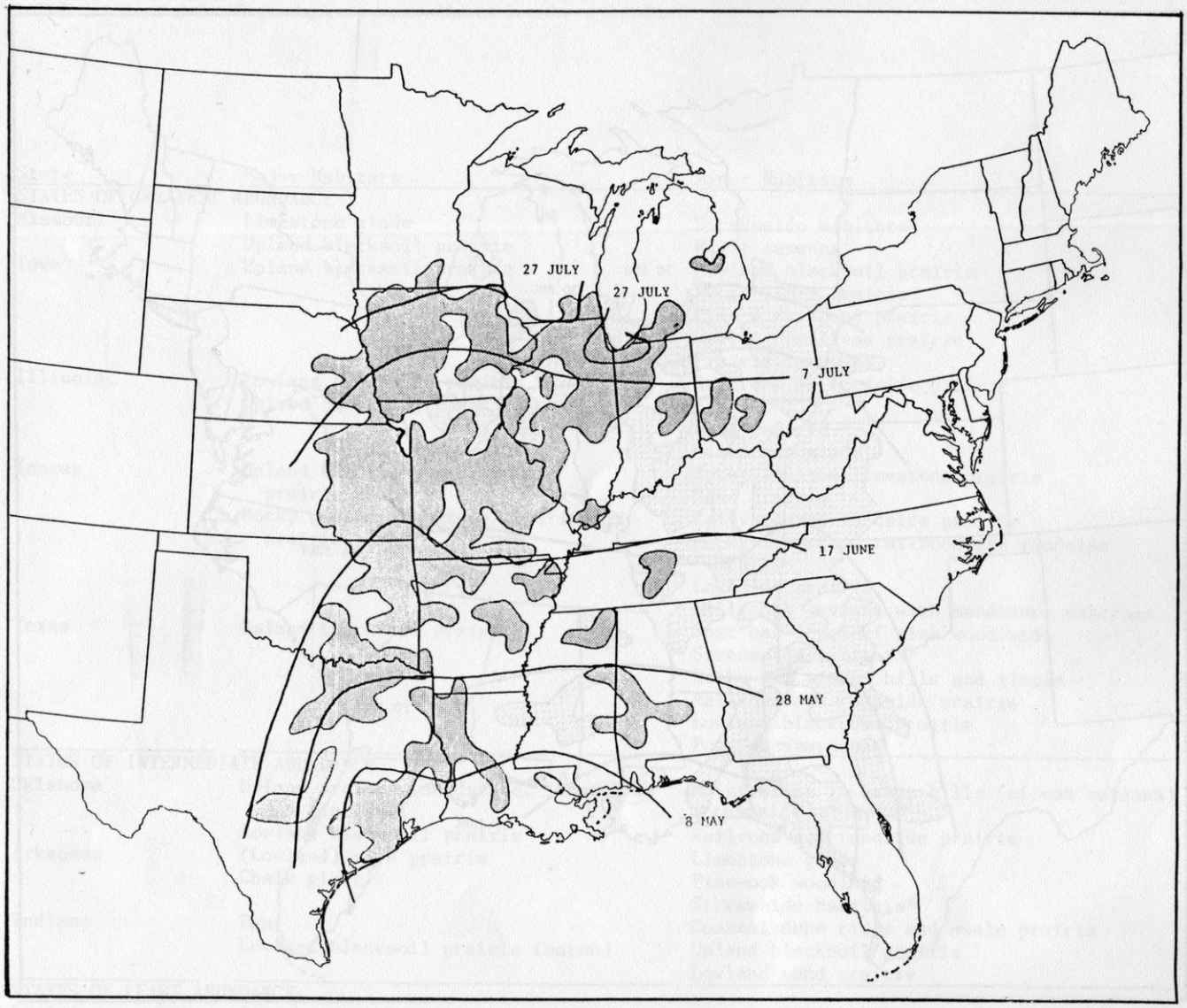

FIG. 3. Period of flowering of *Cacalia plantaginea* throughout its range.

1891, Deam 1940, Fitzpatrick 1899, Lowe 1921, MacMillan 1892, Peterson 1912, Smith 1978, Steyermark 1963, Swink and Wilhelm 1979, Voight and Mohlenbrock 1977) for construction of distribution, habitat, and phenological maps. Morphological data obtained from the herbarium specimens included:

1. Basal leaves: Length was measured in cm from tip of blade to juncture of blade taper at petiole; width at the widest point across the blade, perpendicular to the veins. Where it was evident that leaf blades had shrunken in drying, apparent by stain of original leaf outline on the paper, measurements were made from the latter. Leaf blades with significant broken or chewed areas were reconstructed for measurements.
2. Inflorescence: The lowest branch, whose flower heads were a part of the main, flat-topped cymose inflorescence was measured in cm. The assumption was made that the length of this branch was positively related to inflorescence and plant size (Athey and Pippen, unpubl.). Length, from the juncture of the branch and main stem to the top of the center capitulum of the cymule at the end of the branch, and width, taken 0.5 cm from the stem, were measured and recorded.
3. Stem: The size of the stem was interpreted as an indicator of the robustness of the plant (Athey and Pippen, unpubl.). Length, from the old leaf scars at ground level to the top of the heads at the center of the inflorescence, and width, at 5-6 cm above ground level were measured in cm and recorded.

Data Analysis

Using location data from herbarium specimens and published floras, a distribution map by county (Fig. 1) was constructed. From this a general range map was drawn (Fig. 2). Dates of full bloom (Fig. 3) and seed maturity (Fig. 4) were plotted on an overlay of the distribution map and isophenes were drawn connecting dots of equal phenology across the range. The medians of blooming and seed maturity dates, in the zones between isophenes, were determined and compared to establish the number of days from bloom to seed maturity (Table 1).

The habitat of *Cacalia plantaginea* in each state was characterized using habitat information from herbarium sheets and published floras (Table 2). This information was summarized in a habitat map (Fig. 5). Habitats were tallied for each state as major (a habitat

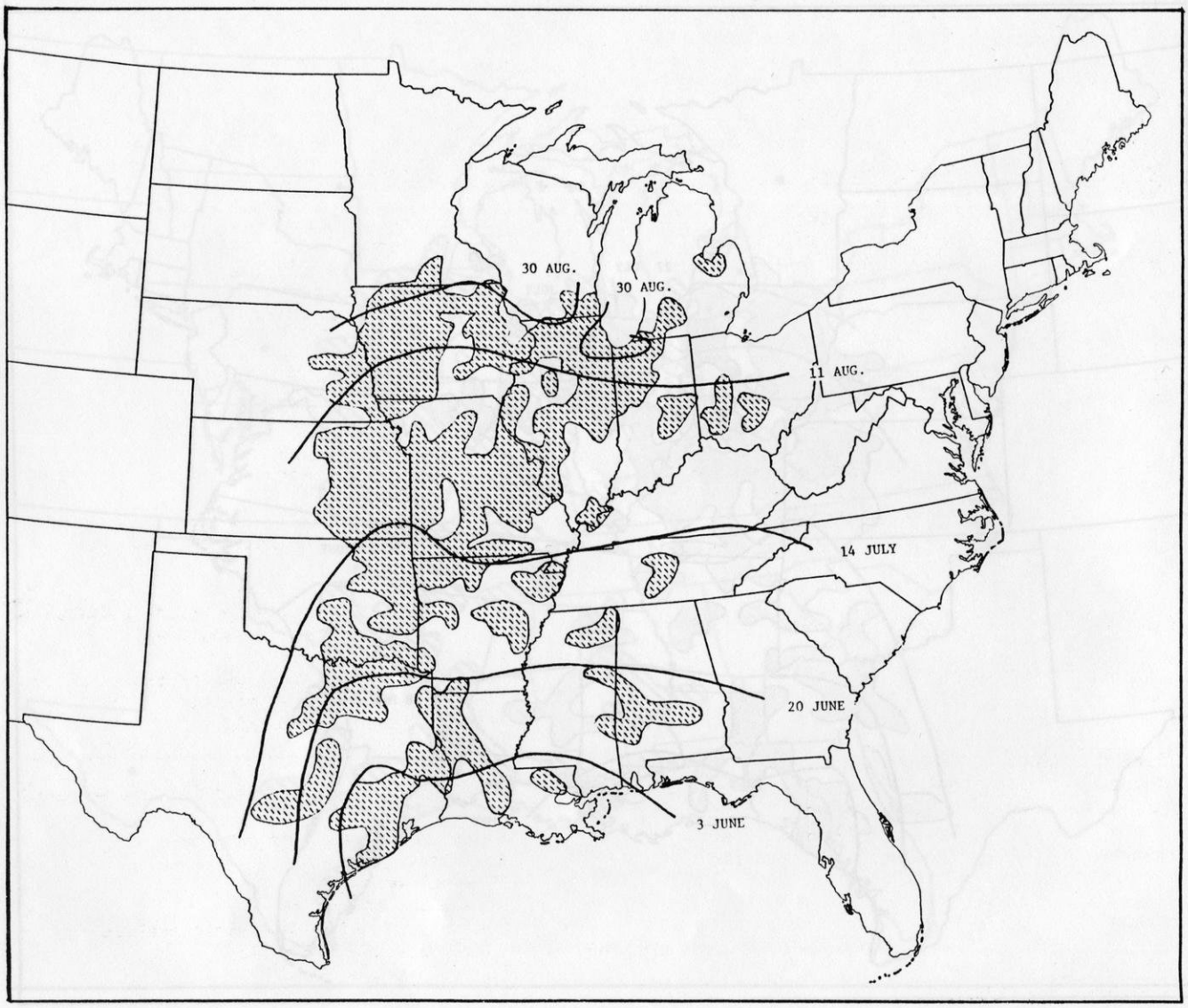

FIG. 4. Date of seed maturity of *Cacalia plantaginea* throughout its range.

containing more than 25 percent of specimens) and minor (all other non-artificial, non-weedy habitats) (Table 3). Roadsides and railroads were included if "prairie" or "grassland" was an epithet. The numerical center of the range of *C. plantaginea* was determined from the number of counties of occurrence and number of specimens in each state.

Statistical Tests

For statistical purposes we assumed that the collections of *Cacalia plantaginea* specimens from the various herbaria were random across the plant's range. Using the habitat data (Table 2) and habitat map (Fig. 6), *C. plantaginea*'s range was divided into a series of habitat regions shown in Table 4. The mathematical means of the morphological data for the habitat regions (Tables 4 and 5) were compared statistically. Stepwise Discriminant Analysis was used to determine the best discriminating variable to account for differences in plants between regions. Hotelling's T-test was used to determine the significance ($\alpha = 0.05$) of each comparison. Height of plant and length of inflorescence branch were used to compare size of plants growing in northern lowland and upland habitats using Hotelling's T-test ($\alpha = 0.05$) to determine if soil moisture availability had an effect upon plant size.

RESULTS

In comparison of leaf sizes (Table 6), plants at the northeastern edge of the range have significantly narrower basal leaves than plants in all other parts of the range. Plants in the north central part of the range have significantly narrower basal leaves than those along the southern edge of the range. Leaf blades of plants in the northwestern part of the range are significantly shorter than those of plants growing in cedar glades of Arkansas, Missouri and Texas. Plants in the northwestern part of the range also have significantly shorter basal leaf blades than plants in fens at the northeast edge of the range.

No significant differences in size exist between plants growing in moist and dry sites in the northern part of the range. This suggests that moisture is not a limiting factor to size at the northern limit of the range and that specimen data from dry and moist habitats in a region may be combined.

Plants in the northern part of the range have significantly smaller

TABLE 2. Habitat of *Cacalia plantaginea* by state. Habitat in order of abundance.

State	Major Habitats	Minor Habitats
STATES OF GREATEST ABUNDANCE		
Missouri	Limestone glade	Streamside habitats*
	Upland blacksoil prairie	Hilly savanna
Iowa	Upland blacksoil prairie	Lowland blacksoil prairie
		Loess bluff prairie
		Upland railroad prairie
		Lowland railroad prairie
		Prairie cemetery
Illinois	Lowland blacksoil prairie	Railroad or roadside prairie
	Upland blacksoil prairie	Fen
		Sand prairie
		Limestone glade
Kansas	Upland blacksoil prairie and prairie pasture	Rocky lowland limestone prairie
		Sand prairie
	Rocky upland limestone prairie and prairie pasture	Railroad and roadside prairie
		Rocky limestone railroad and roadside prairie
		Lakeside prairie
		Hilly oak savanna with sandstone outcrops
Texas	Upland blacksoil prairie	Post oak-longleaf pine woodland
		Streamside habitats*
		Rocky calcareous hills and slopes
		Railroad and roadside prairie
		Lowland blacksoil prairie
		Post oak savanna
STATES OF INTERMEDIATE ABUNDANCE		
Oklahoma	Upland prairie, sandstone, limestone, and blacksoil	Moist sites in sandy hills (of oak savanna)
		Streamside habitats*
	Lowland blacksoil prairie	Railroad and roadside prairie
Arkansas	(Lowland) rice prairie	Limestone glade
	Chalk glade	Pine-oak woodland
		Streamside habitats*
Indiana	Fen	Coastal dune ridge and swale prairie
	Lowland blacksoil prairie (marsh)	Upland blacksoil prairie
		Lowland sand prairie
STATES OF LEAST ABUNDANCE		
Louisiana	Sandy post oak-longleaf pine or longleaf pine woodland	Coastal plain (grassland)
		Upland (blacksoil) prairie
	Upland railroad or roadside prairie	
Nebraska	Lowland blacksoil prairie	Rocky upland prairie (sandstone)
	Upland blacksoil prairie	Sand prairie
Michigan	Fen	Coastal dune ridge and swale prairie
		Coastal calcareous cobble beach
Ohio	Fen	--
Mississippi	--	Upland blacksoil prairie
		Oak woodland over limestone bedrock
Alabama	Upland blacksoil prairie	Chalk prairie
		Rich woodland
Wisconsin	Lowland prairie	Fen
		Lowland sand prairie
		Coastal dune ridge and swale prairie
Ontario	--	Coastal calcareous interdunal wetland
Minnesota	"...damp prairies and openings" (McMillan, 1882)	--

* Streamside habitats include "thickets," "meadows," and perhaps lowland prairies.

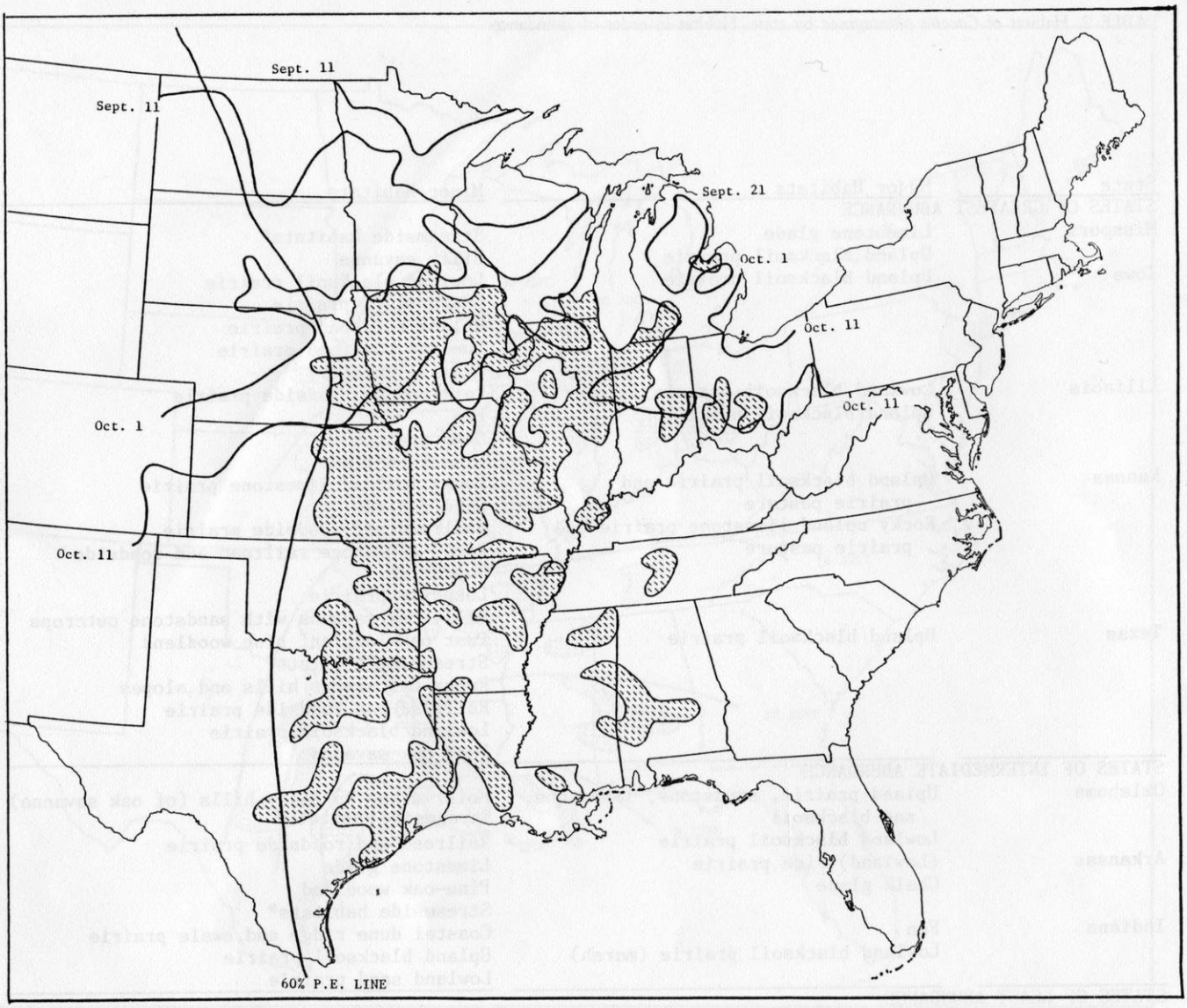

FIG. 5. Dates of first killing frost and 60% P:E line superimposed over the range of *Cacalia plantaginea*.

inflorescences than plants in the southern part of the range (Table 7). Plants in the northwest edge of the range are significantly shorter than in any other part of the range except the southeast edge (Table 7). Plants at the range center were not always larger than plants at range edge. For example, compare the stem length and inflorescence branch length of plants in the south-center to those in the far east edge of the range (Table 7, Region 3 to 2) and south-center to south edge (Table 7, Region 3 to 8).

Cacalia plantaginea is a plant of the tallgrass prairie (Table 2 and Fig. 6). Most (17/23) of the major habitats, especially in the numerical center of its range (Table 3), are tallgrass prairie habitats, mainly upland and lowland blacksoil prairie. Except for the post oak-longleaf pine woodlands of Louisiana and Texas, other major habitats - fen and limestone (and chalk) glades - are related to tallgrass prairies. Most (26/48) minor habitats are tallgrass prairie habitats (on a variety of substrates), and many of the remainder are related to tallgrass prairie (e.g., oak savanna).

DISCUSSION

The results show that plants of *Cacalia plantaginea* in the northern part of its range tend to have smaller inflorescences and more restricted basal leaf sizes. At the north edge of the range plants experience cooler temperatures during a shorter growing season. In a species such a *C. plantaginea* which apparently originated in the Ozark region (Table 3) a shorter growing season could slow development. Smaller inflorescences are interpreted as an attempt to shorten the time between onset of the growing season and full bloom, thus compensating for a longer development time between full bloom and seed maturity. Development from full bloom to seed maturity requires 21-25 days in the south half of the range and 33-35 days in the north half (Table 1). Therefore, the factors limiting *C. plantaginea* at the north edge of its range are probably fewer growing degree days (which slows overall growth as well as seed development) and time of first killing frost (which arrests development of seed in individuals that have not matured their seeds) (Fig. 4 and 5). McCann (1979) indicated that growing degree days were a significant factor in establishing the northern limit of southern plants in Michigan.

The western limit of the range of *C. plantaginea* corresponds well with the 60% P:E line (Fig. 5) and the western edge of the tallgrass prairie. We suspect that water stress is crucial to the western limit of the species. In the northwest part of the range, lower precipitation and greater evaporation may produce greater

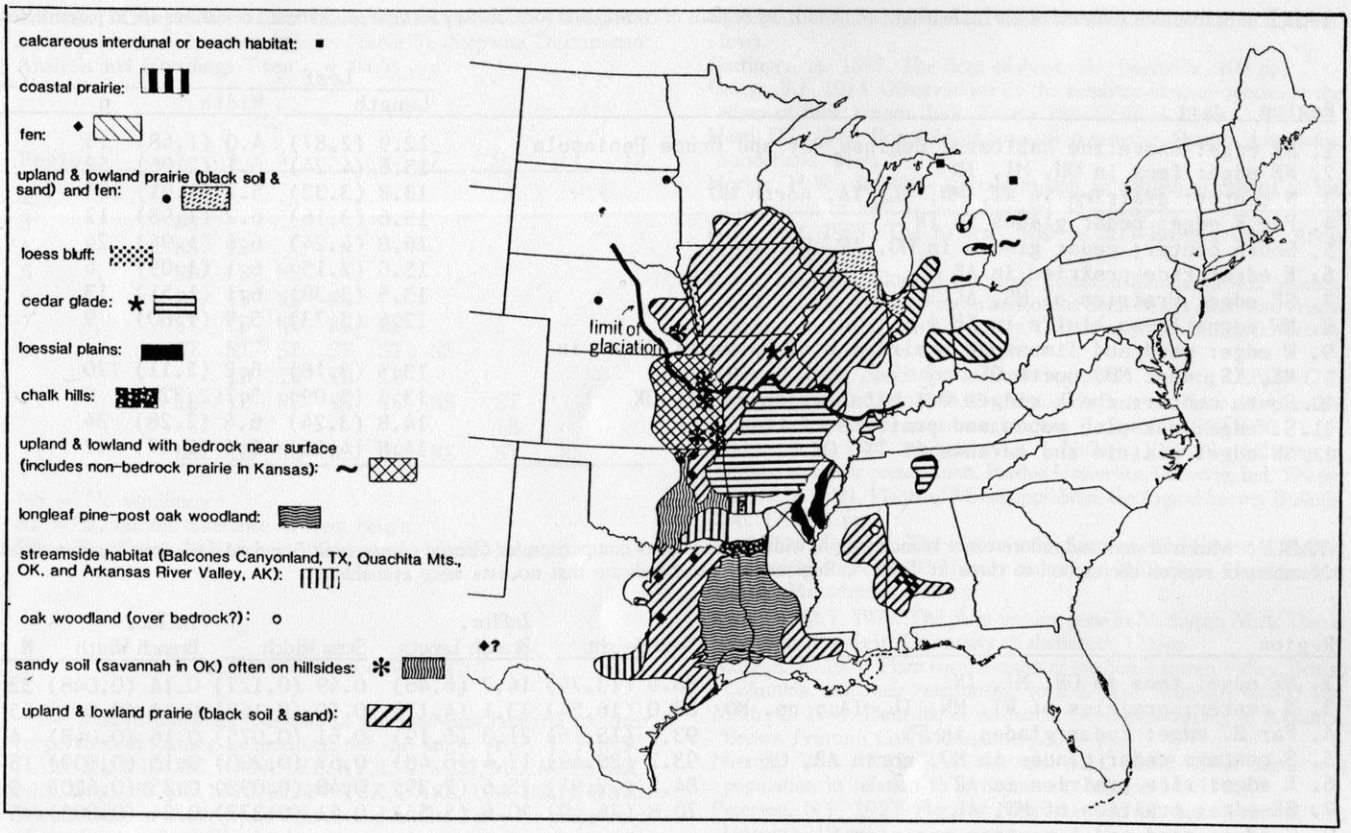

FIG. 6. Major and significant minor habitats of *Cacalia plantiginea*.

TABLE 3. Number of counties, sites, and major and minor habitats for *Cacalia plantaginea* by state.

State	No. of counties	No. of sites (from specimens)	No. major habitats	No. minor habitats
STATES OF GREATEST ABUNDANCE				
Missouri	55	50	2	2
Iowa	54	73	1	5
Illinois	48	67 (26 from Cook Co)	2	4
Kansas	45	107	2	6
Texas	41	50	1	6
STATES OF INTERMEDIATE ABUNDANCE				
Oklahoma	28	26	2	3
Arkansas	25	18	2	3
Indiana	18	33	2	3
STATES OF LEAST ABUNDANCE				
Louisiana	13	23	2	2
Nebraska	12	28 (6 from Lincoln)	2	2
Michigan	11	11	1	2
Ohio	9	21	1	–
Mississippi	8	5	–	2
Alabama	7	11	1	2
Wisconsin	6	10	1	3
Ontario (Canada)	4	17	–	3
Minnesota	4	1	1	–
South Dakota	1	0	–	–

TABLE 4. Mathematical means of leaf blade length and width, by regions of comparison for *Cacalia plantaginea*. Standard deviations are in parentheses.

Region	Leaf Length	Leaf Width	n
1. NE edge: shoreline habitats, Saginaw Bay and Bruce Peninsula	12.9 (2.87)	4.0 (1.68)	15
2. NE edge: fens in OH, MI, IN	15.6 (4.24)	6.1 (2.06)	52
3. N center: prairies in WI, MN, IL, IA, north MO	13.8 (3.32)	5.7 (1.91)	106
4. Far E edge: cedar glades in TN	15.6 (3.16)	6.2 (1.98)	12
5. South center: cedar glades in MO, AR, OK	16.8 (4.24)	6.6 (1.94)	24
6. E edge: rice prairies in AR	15.6 (2.15	6.1 (1.09)	6
7. SE edge: Prairies of MS, AL	15.5 (3.38)	6.1 (1.51)	13
8. NW edge: loess bluffs in NE	12.6 (3.73)	5.9 (1.80)	9
9. W edge: sand and limestone prairies W of Missouri River in NE, KS, west MO, north OK	13.5 (3.18)	6.2 (2.11)	120
10. South center: chalk ridges Ouichita region in AR, OK	13.3 (3.09)	5.7(2.32)	6
11. S. edge: oak-pine woods and prairies of LA, TX	14.8 (3.24)	6.4 (2.28)	34
12. SW edge: prairie and savanna of TX, OK	14.8 (4.65)	6.4 (2.47)	42

TABLE 5. Means of stem and inflorescence branch length, width by regions of comparison for *Cacalia plantaginea*. Standard deviations in parentheses. Numbers of regions correspond to those in Table 4. Regions not listed indicate that no data were available.

Region	Stem Height	Inflor. Branch Length	Stem Width	Inflor. Branch Width	N
2. NE edge: fens in OH, MI, IN	86.9 (13.74)	14.7 (6.46)	0.49 (0.127)	0.14 (0.048)	32
3. N center: prairies of WI, MN, IL, IA., no. MO	83.0 (16.54)	13.1 (4.17)	0.50 (0.162)	0.13 (0.042)	65
4. Far E. edge: cedar glades in TN	93.9 (15.16)	21.3 (6.19)	0.61 (0.075)	0.16 (0.048)	4
5. S center: cedar glades in MO, north AR, OK	93.2 (30.49)	17.4 (5.48)	0.57 (0.200)	0.15 (0.039)	13
6. E edge: rice prairies in AR	84.2 (7.91)	15.6 (2.39)	0.48 (0.093)	0.35 (0.620)	9
7. SE edge: prairies of MS, AL	70.8 (26.40)	20.6 (5.55)	0.61 (0.277)	0.24 (0.096)	5
9. W edge: sand and limestone prairies W of Missouri River in NE, KS, w. MO, no. OK	69.5 (14.79)	14.6 (4.23)	0.54 (0.151)	0.16 (0.212)	80
11.S. edge: oak-pine woods & prairies of LA, TX	85.8 (17.28)	19.5 (6.66)	0.58 (0.180)	0.17 (0.063)	27
12. SW edge: prairie & savanna of OK & TX	84.0 (13.23)	15.3 (5.82)	0.56 (0.130)	0.17 (0.085)	22
MEAN, ALL REGIONS	79.8 (16.73)	15.2 (4.98)	0.53 (0.157)	0.16 (0.175)	235

TABLE 6. Comparisons of leaf dimensions of *Cacalia plantaginea* growing in all twelve habitat regions (Table 4). (Stepwise Discriminant Analysis and Hotellings T-test, = 0.05).

Region	1	2	3	4	5	6	7	8	9	10	11	12
2	S											
3	BW	BL										
4	S	NS	NS									
5	S	NS	BL	NS								
6	S	NS	NS	NS	NS							
7	S	NS	NS	NS	NS	NS						
8	BW	BL	NS	NS	BL	NS	NS					
9	BW	BL	NS	BL	BL	NS	NS	NS				
10	NS	NS	NS	NS	NS	NS	NS	NS	NS			
11	BW	NS	BW	NS	NS	NS	NS	NS	NS	NS		
12	BW	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	

NS = No significant difference among pairwise variables.
BW = Differ with respect to leaf blade width.
BL = Differ with respect to leaf blade length.
S = Significantly different among pairwise variables.

water stress, which, coupled with a short growing season, could produce very short plants.

Factors common to most habitats are lack of canopy or heavy shrub cover (22/23 major, 40/48 minor habitats) and circumneutral to moderately alkaline soils or substrates (21/23 major, 29/46 minor habitats) (Table 2).

In much of the range (AR, OK, MO, KS, NE, IA, IL) upland habitats are more common than lowland, but lowland habitats are very important and plants of upland situations may occupy the moistest places available.

Habitats at the northeast and northern edges (ONT, MI, OH, IN, WI, MN) are nearly all wetlands. Habitats at the southeast and southern edges are nearly all upland (AL and MI exclusively; LA and TX mostly). Habitats at the eastern edge of the range (ONT, MI, OH, IN, S. IL, TN, AL, MS) are all calcareous.

The factor restricting the distribution of *Cacalia plantaginea* in the forested east part of its range is apparently the availability of open calcareous habitats (which are wet in the north and dry in the south). *Cacalia plantaginea* appears to be an obligate calciphile in the east part of its range (but not along its west edge). It may be that the only suitable open habitats available there also happen to be calcareous; in any case, no conclusion on this matter can be drawn from our data.

Habitat restriction is interpreted here to be a reduction in the number of major and minor habitats by state. There are only one or two major habitats in each state throughout the range, with only one along the eastern edge. There are four to six minor habitats in the center of the range (except in Missouri where only two occur) but only two or three throughout the rest of the range. In summary, there may be more minor habitats in the center of *C. plantaginea*'s range, but the exceptions noted above, and the lack of statistical tests for habitat restriction make any conclusion highly tenuous. Habitat restriction may be illusory, apparent evidence of it being the simple consequence of prevailing regional vegetation types rather than any internal mechanism in the plant.

An outlier in Jeff Davis Co., Texas, 280 miles southwest of the westernmost extension of the range, occupies dolomitic hills, knobs, and slopes, and may reflect a more westerly distribution for *Cacalia plantaginea* during Pleistocence glaciation when the climate was cooler and moister.

TABLE 7. Comparisons of size characteristics of *Cacalia plantaginea* growing in selected habitat regions (Table 5). (Stepwise Discriminant Analysis and Hotellings T-test, = 0.05).

Region	2	3	4	5	6	7	9	11	12
2									
3	NS								
4	NS	IB							
5	NS	IB	NS						
6	NS	IB	NS	NS					
7	ST	IB	NB	NS	NS				
9	ST	ST	ST	ST	ST	NS			
		IB	IB	IB	IB				
11	IB	IB	NS	NS	NS	NS	ST		
							IB		
12	NS	IB	NS	NS	NS	NS	ST	NS	

NS = No significance.
ST = Significant difference in stem height.
IB = Significant difference in inflorescence branch length.

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FLORISTIC AND VEGETATIONAL SURVEY OF THE W. PEARL KING PRAIRIE GROVE, A PRAIRIE REMNANT IN MADISON COUNTY, OHIO

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Abstract. A 5.6 hectare prairie, the W. Pearl King Prairie Grove, near Mechanicsburg, Ohio, is co-dominated by *Andropogon scoparius* and *Sorghastrum nutans* and contains more than 25 additional prairie species. The vegetation was sampled by the use of 424 1-m² quadrats through which percent cover, frequency, and commonness values were determined. A grid system was utilized in producing a map of the extant vegetation. Six distinct vegetation communities occur there. One area is dominated by *Sporobolus heterolepis*, an endangered species in Ohio. Diversity and percent cover of prairie indicator forbs are low, while frequency and density of the grasses are high. Past land uses such as grazing and annual burning may be partially responsible for the present species composition. Woody species include *Quercus macrocarpa*, *Q. stellata*, and *Q. alba*, some specimens of which exceed 300 years in age. From evidence gathered within the study area, i.e., soil characteristics, antiquity of trees, and presence of *Sporobolus heterolepis*, the site appears to be original prairie that has never been cultivated. The significance of this endangered prairie type makes it well worthy of inclusion in Ohio's system of state preserves.

INTRODUCTION

The W. Pearl King Prairie Grove appears on the map of the Prairie Peninsula prepared by Transeau (1935) which depicts an eastward extension of tallgrass prairie into the deciduous forest of west-central Ohio. This geographical region, with a prairie-hardwood forest mosaic, was given the folk name "Darby Plains" by early pioneers. Over the past 100 years, the Darby Plains, with an area of approximately 1,000 square kilometers (385 square miles), have undergone great transition from prairie and forest to an area dominated by corn, wheat, and soybean fields. Interspersed throughout this "new" vegetational cover are widely scattered remnants of original vegetation, primarily tallgrass prairie and mixed-oak woodlots. Because of the presence of numerous disappearing tallgrass prairie species, most notably *Sporobolus heterolepis*, which has been designated an endangered species in Ohio by Cooperrider (1982) and a threatened species in Ohio by McCance and Burns (1984), this study has been undertaken to assess its ecological significance. The primary purposes of this study are: 1) to describe the vascular flora through a systematic survey, and 2) to construct a map of the extant vegetation. The initial proposal and subsequent autumnal study were the efforts of Patti Raley during the fall of 1981. I have since incorporated a substantial amount of additional data into the work of Raley, and developed the following insights on the ecology of the area.

W. Pearl King Prairie Grove is a privately owned mixed-oak, tallgrass prairie community and represents one of the largest (5.6 hectares) prairie remnants in the state. Despite certain disturbances, primarily grazing and annual burning, the prairie species have fared quite well and the site still retains the aspect of high quality tallgrass prairie. The site is located seven kilometers southeast of Mechanicsburg in the northwestern corner of Monroe Township, Madison County, Ohio, immediately west of the intersection of David Brown Road (Madison County Road 119) and Mechanicsburg-Sanford Road (Madison County Road 27). The elevation is approximately 336 meters with a latitude of 40° 02′30″N and a longitude of 83° 28′W. The study area lies within the glaciated section of the Central Lowland Province with the underlying bedrock composed of Upper Silurian dolomites of the Bass Islands group (Foley 1973). The overall topography of the region is a nearly level to slightly undulating ground moraine. Soil series are of the Kokomo-Crosby-Lewisburg association consisting of nearly level to gently sloping, poorly drained to moderately well-drained soils that developed in late Wisconsinan-age clay loam till (Gerken and Scherzinger 1981). Specifically, the site has been mapped (Gerken and Scherzinger 1981, Sheet nos. 6 and 10) with equal amounts of Kokomo silty clay loam and Crosby-Lewisburg silt loam. The climate classification is humid-continental with an average temperature of 10° C and an annual precipitation of approximately 95 centimeters (Ruffner and Bair 1977). The original or potential natural vegetation cover has been mapped as a mosaic of mixed tallgrass prairie and oak-hickory forest by Kuchler (1966), and as prairie grassland by Gordon (1966).

MATERIALS AND METHODS

Methods originally used by Raley were slightly modified, and selected to display statistically the floristic composition of the area. Specimens of vascular plants are on deposit in The Ohio State University Herbarium.

In order to facilitate the sampling procedures and expedite the mapping process, a grid system was established in the study area. The grid lines (transects) extend parallel to the two longest sides, i.e., the northwest and the northeast sides (Fig. 1). A handheld compass was used for the directional orientation and a one-meter pace was used for measurements.

Using the intersecting transect lines as reference points, the 1-m² quadrats were spaced equally along these lines, i.e., wherever two lines intersected, a quadrat was placed. Within each quadrat all vascular plants were noted. Species names and number of stems, or approximate percent cover, were also determined. A total of 424 1-m² quadrats, representing approximately three percent of the total study area, were sampled. From quadrat information, percent cover, frequency, and commonness values were determined using methods adopted from Curtis (1959).

The grid system was also used in constructing a map of the major cover types occurring at the site. Sampling along the transect lines made it possible to discern one major cover type from the next. These major changes of cover type were approximately marked on a field map which was subsequently used in production of the final map (Fig. 1).

The study area was observed an average of two times per month, starting in early June and terminating late October. Community sampling procedures were initiated in early June, and continued into September. During each visit, the area was carefully examined for plant species not previously seen in the study site. Identifications of plants were determined using Gleason and Cronquist (1963) and Weishaupt (1971). Nomenclature follows Fernald (1950).

Ten trees with diameters of 50 centimeters or greater were randomly selected by use of the field map which depicted their location within the study area. Subsequently, these trees were located within the study area. Heights, diameters and cores were obtained from each specimen.

RESULTS

Sixty-five species representing 28 families were encountered in the 424 quadrats. Table 1 separates the quadrat sampling plots

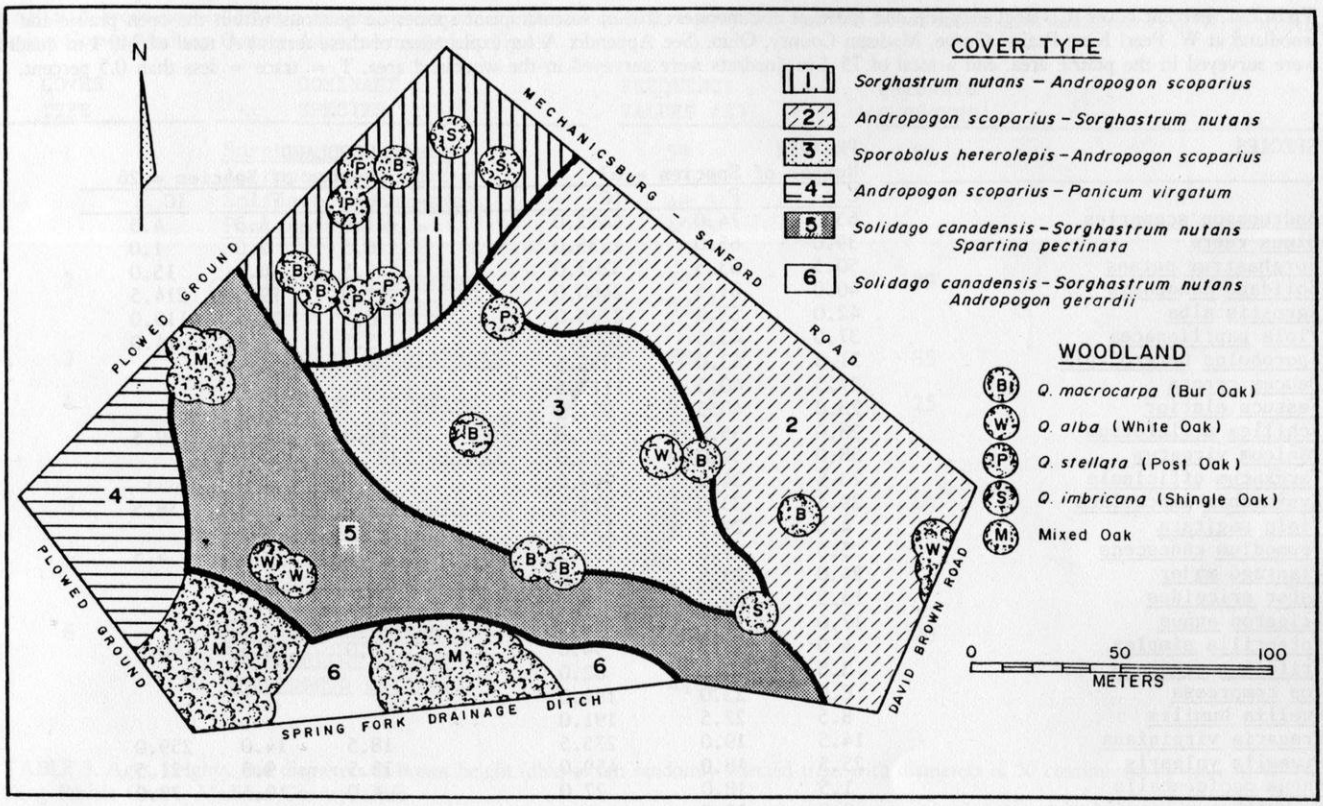

FIG. 1. Major cover types and locations of woody species at W. Pearl King Prairie Grove, Madison County, Ohio.

into two distinct zones. One is the open prairie. The second represents the woodland quadrats, or those quadrats located at least in part within a tree's drip line in case of a single specimen. The change from open prairie to woodland is abrupt and quite distinct. *Andropogon scoparius* is the dominant species in the open prairie with a frequency of 71 percent. This species is almost non-existent in the semi-shaded to totally shaded woodland areas, with a frequency of 4.5 percent. On the other hand, *Rubus allegheniensis* is the most frequent woodland species with a frequency of 44 percent (open prairie frequency 2.5 percent). *Agrostis alba* is the most frequent woodland grass with a frequency value of 13.5 percent. *Solidago canadensis* is the most represented forb in both the open prairie and woodland communities, with frequencies of 44 percent and 32 percent, respectively.

Throughout the duration of this survey, a total, of 113 species representing 36 families was recorded. Thirty-one prairie indicator species are represented there. A diverse array of seven prairie indicator grasses is also present at the site. *Sporobolus heterolepis* occurs in healthy, vigorous stands with a frequency of 31.5 percent. Of a total of 24 prairie indicator forbs, *Pycnanthemum virginianum* has the highest frequency, 17.5 percent.

Of the 113 species, 27 are classified as "naturalized" or "adventive" species, meaning they are non-native. Several of these species, *Poa compressa* and *Daucus carota*, for example, are major components of the study area with frequency values of 23 percent and 40.5 percent, respectively.

Six major vegetational cover types are represented within the study area. Fig. 1 displays these cover types and their dominant plant species. A species is considered dominant if the frequency value within that particular community exceeds 50 percent. Table 2 separates each cover type into the frequency values for individual dominants. For example, the largest cover type, area two, is dominated by an *Andropogon scoparius-Sorghastrum nutans* association with frequency values of 79 percent and 52 percent, respectively. The core of the area is dominated by an impressive stand of *Sporobolus heterolepis* with a value of 88 percent.

Ten trees with diameters of 50 centimeters or more were randomly selected from the field map and located within the study area. The selected specimens are listed in Table 3 with their ages, heights, and diameters at breast height (dbh). The ten chosen specimens all belong to the genus *Quercus*. The oldest of the ten trees is a 340-year-old bur oak (*Q. macrocarpa*) with a height of 21.4 meters and a dbh of 1.43 meters.

DISCUSSION

One of the most notable aspects of this prairie remnant is the lack of prairie indicator forbs commonly occurring on other relict prairies in the Darby Plains. The site has apparently never been cultivated (Tomko and Hall 1982). However, according to Chester Clime (personal communication 1982), owner of the grove, the area was grazed for a number of years. Nyboer (1981) has compiled extensive data in reference to the impact of grazing on Illinois hill prairies. He has concluded that prolonged grazing has a tendency to reduce native species frequency and diversity. At the same time, alien grasses and forbs readily replace the native species. Being highly competitive, the alien species invade and are able to compete well in grazed situations. A similar situation is evident at the King site. The lack of prairie forbs in terms of diversity and frequency, and the abundance of alien and common old field species in the study area tend to parallel Nyboer's findings. Similar results have been reported in other grazed prairie communities by a number of researchers, including Drew (1947) and Evers (1955).

In contrast to the low forb frequency is the diverse assemblage of prairie grasses. Clime (personal communication 1982) reports

TABLE 1. Percent cover (C), frequency (F), and index of commonness (IC) of vascular plant species on quadrats within the open prairie and the woodland at W. Pearl King Prairie Grove, Madison County, Ohio. (See Appendix A for explanation of these terms.) A total of 349 1-m quadrats were surveyed in the prairie area, and a total of 75 1-m quadrats were surveyed in the woodland area. T = trace = less than 0.5 percent.

SPECIES	PRAIRIE Number of Species = 67			WOODLAND Number of Species = 26		
	C	F	IC	C	F	IC
Andropogon scoparius	63.0	74.0	4662.0	1.0	4.5	4.5
Ulmus rubra	39.0	65.0	2535.0	0.5	2.0	1.0
Sorghastrum nutans	50.5	63.5	3207.0	2.5	6.0	15.0
Solidago candensis	40.0	61.5	2460.0	11.0	19.5	214.5
Agrostis alba	42.0	53.0	2226.0	8.5	13.5	115.0
Viola papilionacea	37.0	43.5	1609.5	3.5	4.0	14.0
Sporobolus heterolepis	31.5	43.0	1355.5			
Daucus carota	27.5	40.5	1113.5			
Festuca elatior	23.0	40.5	931.5			
Achillea millefolium	28.0	35.0	980.0	11.0	14.5	159.5
Panicum virgatum	38.0	34.0	1292.0			
Taraxacum officinale	23.5	34.0	799.0			
Lysimachia lanceolata	29.5	33.0	973.5	5.5	7.0	38.5
Viola sagitata	4.5	29.5	132.5			
Desmodium canescens	5.5	29.0	159.5	1.5	3.0	4.5
Plantago major	24.0	28.5	684.0			
Aster ericoides	13.5	28.0	378.0			
Erigeron annus	17.0	26.5	450.5			
Potentilla simplex	4.0	23.5	94.0	3.0	13.5	40.5
Trifolium pratense	3.5	23.5	82.0			
Poa compressa	8.0	23.0	184.0			
Ruellia humilis	8.5	22.5	191.0			
Fragaria virginiana	14.5	19.0	275.5	18.5	14.0	259.0
Prunella vulgaris	25.5	18.0	459.0	13.5	9.0	121.5
Rubus occidentalis	1.5	18.0	27.0	4.0	19.5	78.0
Pycnanthemum virginianum	8.0	17.5	140.0			
Ambrosia tritida	1.5	17.0	25.5	1.0	8.5	8.5
Apocynum cannabinum	9.5	16.0	152.0	4.5	12.0	54.0
Lobelia spicata	2.5	15.0	37.5			
Spartina pectinata	5.5	14.5	79.5			
Setaria glauca	0.5	14.5	7.0			
Vernonia gigantea	1.5	14.0	21.0			
Plantago lanceolata	2.0	13.5	27.0			
Lactuca canadensis	0.5	13.5	7.0			
Ambrosia artemissiifolia	0.5	13.0	6.5			
Solidago graminifolia	1.5	12.5	19.0			
Cirsium discolor	3.5	12.0	42.0			
Sanicula canadensis	9.0	11.5	103.5	17.0	14.5	246.5
Geum canadensis	17.0	11.0	187.0			
Medicago lupulina	1.0	11.0	11.0			
Phleum pratense	17.0	9.5	161.5	15.0	8.0	120.0
Poa pratensis	1.5	9.5	14.0	3.0	6.5	19.5
Andropogon gerardi	5.0	8.0	40.0			
Agrimonia pubescens	2.5	7.0	17.5	4.0	12.5	50.0
Panicum languginosum	0.5	7.0	3.5			
Sambucus canadensis	0.5	7.0	3.5	1.5	10.0	15.0
Carex scoparia	1.5	6.5	10.0			
Rosa multiflora	0.5	6.5	3.0	1.0	9.0	9.0
Carya ovata	1.0	4.0	4.0			
Rubus allegheniensis	0.5	3.0	1.5			
Lycopus virginicus	0.5	2.5	1.0			
Trifolium procumbens	0.5	2.5	1.0			
Galium concinnum	0.5	2.5	1.0	1.0	7.5	7.5
Hypericum punctatum	0.5	1.5	1.0			
Cirsium arvense				13.0	21.5	279.5
Cirsium vulgare	T	0.5		1.5	10.0	15.0
Panicum boscii	T	0.5				
Elymus canadensis	T	0.5				
Quercus imbricaria	T	0.5				
Oxalis stricta	T	0.5				
Lezpedeza violacea	T	0.5				
Galium boreale	T	0.5				
Oenothera biennis	T	0.5				
Aster lowrieanus	T	0.5				
Arctium minus	T	0.5				
Aster novae-angliae	T	0.5				
Carex sp.	T	0.5				
Antennaria plantaginifolia	T	0.5				

TABLE 2. Frequency values of dominant species and number of quadrats surveyed in each of the six major plant communities of W. Pearl King Prairie Grove, Madison County, Ohio, as mapped in Fig. 4.

COVER TYPE	DOMINANT SPECIES	FREQUENCY VALUES (%)	QUADRATS SURVEYED
1	Sorghastrum nutans	59	66
	Andropogon scoparius	53.5	
	Solidago canadensis	48.5	
	Panicum virgatum	40.5	
2	Andropogon scoparius	79	129
	Sorghastrum nutans	52.5	
3	Sporobolus heterolepis	88	85
4	Andropogon scoparius	64.5	25
	Panicum virgatum	47	
	Sporobolus heterolepis	40.5	
5	Solidago canadensis	75.5	99
	Sorghastrum nutans	58	
	Spartina pectinata	43	
	Panicum virgatum	40.5	
6	Solidago canadensis	63.5	20
	Sorghastrum nutans	52	
	Andropogon gerardii	41.5	

TABLE 3. Ages, heights, and diameters at breast height (dbh) of ten randomly selected trees with diameters of 50 centimeters or more in W. Pearl King Prairie Grove, Madison County, Ohio.

	SPECIES	AGE (years)	HEIGHT (meters)	DIAMETER (meters)
1.	Quercus macrocarpa	221	22.1	1.30
2.	Quercus macrocarpa	183	18.2	1.15
3.	Quercus alba	195	20.0	1.70
4.	Quercus stellata	289	18.7	1.35
5.	Quercus macrocarpa	275	14.7	.95
6.	Quercus macrocarpa	245	17.3	1.05
7.	Quercus macrocarpa	225	18.9	1.21
8.	Quercus stellata	325	18.4	.97
9.	Quercus macrocarpa	340	21.4	1.43
10.	Quercus alba	195	16.3	.79
	Average	249	18.6	1.19
	Mean	261	18.4	1.11

that the site has been burned every year for at least the past eight years to eliminate unwanted species, i.e., *Rubus* spp. and *Rosa multiflora*. This inadvertent prairie management technique has undoubtedly been beneficial to the outstanding expression of prairie grasses. Huston (1981), in his study on the effects of burning native prairie, reported that annual burning tends to benefit grass species while depressing the occurrence of certain forbs, especially the annual forbs. Other studies dealing with both native and planted prairies further substantiate the concept that annual burning tends to favor the grasses over the less competitive forbs (Moeller 1973).

The index of commonness is a mathematical measurement which shows the importance of a species to the overall community. As discussed earlier, *Andropogon scoparius* with an I.C. value of 4662 is the most abundant species at the site. Three other grassland species falling within the 10 most frequent species include *Sorghastrum nutans* (I.C. 3207), *Sporobolus heterolepis* (I.C. 1355) and *Panicum virgatum* (I.C. 1292). No tallgrass prairie indicator forbs fall within the 10 most frequent species. However, two alien species fall within the top ten. These are *Daucus carota* (I.C. 1113) and *Achillea millefolium* (I.C. 980). These species, however, are generally non-aggressive and probably pose no major threat to the native species at this time.

Although some of the alien grasses and forbs are fairly abundant, they appear to offer no immediate threat to the native flora. However, one species that should be carefully watched is *Festuca elatior*. This alien grass, with a rather high I.C. value of 932, is commonly used as a hay crop and, from my observations, responds favorably to annual burning. With this aspect in mind, continued annual burning could eventually pose a problem in reference to alien plant aggression. This situation needs to be carefully monitored on a yearly basis and management measures taken if warranted.

Tomko and Hall (1982) have compiled extensive data on the soil characteristics of the site. Their endeavors include a soil comparison of samples taken within the study area and from an adjacent cultivated field. They report a distinct difference in the physical and chemical characteristics between the two sets of samples. For example, within the cultivated field bulk densities due to compaction, shows an increase while organic matter levels demonstrate a substantial decline. Chemical changes in the cultivated field include lower amounts of magnesium and increased levels of calcium and potassium due to chemical fertilizer application.

Tomko and Hall (1982) also offer insight to whether the soil

within the study area has ever been cultivated. The first, as discussed above, is the distinct physical and chemical differences between the two soil samples. Another is the presence of *Sporobolus heterolepis* which is highly susceptible to soil disturbance. Other reasons include the presence of large bur and post oak trees and a discussion with the owner who can recall of no disturbance other than grazing (Tomko and Hall 1982). With these factors in mind, they conclude that "there is no evidence that the uncultivated site (W. Pearl King Prairie Grove) has ever been disturbed."

Several species discovered at the site represent new vascular plant records for the Darby Plains. These include: 1) *Scutellaria parvula*, a low-growing mint which occurs as one small clump in the northeast section of the study area, and 2) *Polygala verticillata*, a small inconspicuous member of the Milkwort Family which occurs primarily within the *Sporobolus heterolepis* community among the thick grass clumps. Other infrequent species include *Lythrum alatum*, winged prairie loosestrife, a plant more common in wet than mesic prairies. It occurs in the road ditch adjacent to Mechanicsburg-Sanford Road. *Veronicastrum virginicum* is present in one impressive stand of approximately 40 flowering stems along the north side of the study area. *Galium boreale*, a plant of more northern affinity, grows in one large clump along the western border of the site. The scarcity of certain prairie indicator forbs in terms of total individuals is further evidence of past grazing activity.

Thirteen woody species have been recorded within the study area. Shrubs, except for *Cornus racemosa*, are non-existent. Annual burning has apparently repressed the growth of seedlings and young saplings of the larger woody species, such as *Carya ovata*, *Ulmus rubra*, and *Quercus* spp. *Ulmus rubra*, the most abundant woody species, has an extraordinary frequency of 65 percent and a I.C. value of 2535. However, these figures are misleading and actually over-represent the overall importance of this species. The high values have probably resulted from the annual burning that causes a yearly die back; hence, no specimen larger than one centimeter dbh is present. The widespread occurrence of *U. rubra* throughout the area is an enigma especially since no large parent trees are present within the general area.

The large trees are another important feature of the total prairie community. Eighty-five percent of the trees greater than 25 centimeters dbh are oaks (*Quercus* spp.). Approximately 50 percent of these are bur oaks. Although large oak tree frequency is high, reproduction of oaks is extremely low. During the sampling procedures only one oak seedling was recorded (*Quercus imbricaria*). The lack of young oak seedlings, in light of the high occurrence of parent trees, is not fully understood. Again, annual burning may be the single most important factor in reference to the low germination of oak seedlings.

In review of present conditions at the site, past disturbances, e.g., grazing and annual burning, apparently are the two primary factors responsible for the present floral composition. As stated earlier, the predominating vegetative cover at the site are five species of grasses. The highest ranked prairie indicator forb in terms of I.C. value was *Lysimachia lanceolata*, with a value of 973. The majority of remaining prairie indicator forbs are ranked very low on the list with many displaying I.C. values of less than 50.

This condition appears to be unique for the prairie remnants within the Darby Plains. Most of the major remnant prairie sites remaining in the Darby Plains (Bigelow Cemetery, Smith Cemetery, and Milford Center, see King 1981) have a higher diversity of prairie indicator forbs and also display a more even balance between the grasses and forbs in terms of the number of stems. In fact, the Milford Center site is generally dominated by forbs with grasses being less abundant. These three sites, however, were probably never subjected to the prolonged grazing disturbances which the W. Pearl King site has endured. At one time, the W. Pearl King Prairie Grove possibly resembled the other sites in the Darby Plains with a greater diversity of forbs. On the other hand, the study site could have always been dominated by grasses and may have naturally lacked a diverse array of forbs. However, a transition of floral composition from great diversity toward a domination by several grass species appears to be a subsequent result of past land usage.

SUMMARY

From evidence gathered within the study area, i.e., soil types, plant diversity, species composition, antiquity of the trees, and most importantly the occurrence and vitality of *Sporobolus heterolepis*, W. Pearl King Prairie Grove appears to be an original prairie remnant. Being one of the last remaining eastern outliers of Transeau's famous Prairie Peninsula, this botanical phenomenon is a living history book of natural heritage. It harbors historical, educational, and scientific values that can never again be recreated if the area were destroyed. Virtually all of this area's prairie ecosystems have been obliterated. The elimination of W. Pearl King Prairie Grove would be an irreplaceable loss to society and the renowned diversity associated with the greatness of the Ohio Country. It seems only fair and sensible that an area as significant as this be preserved for all its inherent values.

In retrospect, the Darby Plains in presettlement times contained over several hundred square kilometers of virgin tallgrass prairie. Today, little remains of this ecosystem. These extensive prairie pockets have been reduced to a handful of depauperate remnants, primarily along railroad tracks and in pioneer cemeteries, which more closely resemble museum displays than true prairie communities. The W. Pearl King Prairie Grove is an exception. This area is a coherent, inextricable part of the total landscape that induces a feeling of purity, wholeness, and continuity not found elsewhere in the Darby Plains. Here one can experience the true wonder of the prairie.

To preserve W. Pearl King Prairie Grove as a state nature preserve would be a tremendous stride in the continuing preservation of Ohio's natural heritage. This tract of land is the largest unspoiled and unplowed prairie known to exist in the Darby Plains. An urgent need exists in the intensively cultivated regions of western and central Ohio to preserve biological, genetic and edaphic diversity. Such areas are excellent biometers which scientists can use in measuring the health of the landscape. Generally, a diverse landscape is a healthy landscape. With these ideas in mind, W. Pearl King Prairie Grove is certainly worthy of preservation. If this area is destroyed, the loss to society and posterity would be substantial and irretrievable.

All forms of future management should revolve around maintaining the excellent stand of prairie dropseed which covers approximately one-fifth of the site. Although annual burning has probably enhanced the fine stand of prairie dropseed, the continuance of this practice may have detrimental effects on other species. For example, some of the forbs may be at a disadvantage because each year their seed source may be destroyed and their perpetuation annually thwarted. On the other hand, the grasses are at a distinct advantage because their growth can continue vegetatively by underground rhizomes.

With these factors in mind, it would be wise to discontinue the annual burning and establish a yearly management plan geared towards maintaining the highest possible diversity of species. Without a doubt, this will call for further studies and observations on the exact trends of certain species. The plant community map developed by this study would be instrumental in this respect. Experimental management plans might entail utilizing a diversity of prairie management techniques. Mowing or haying rotation, handcutting of invading woody speices, removal of certain alien species, and burning are some of the possible techniques. Any management program would have to be carefully reviewed and updated in anticipation that the ultimate management objectives are being met.

Public utilization of the area, be it an educational, scientific, or recreational aspect, is another factor that must be addressed.

If the area does become a nature preserve, the primary use of the area would probably be in the form of group visitation. From my observations, it is generally not the curious individual or the casual naturalist who does the damage. It is usually the large groups who mean well, but cause damage to sensitive environments due to their large numbers. In this case, it would be well advised to establish a designated walkway through the preserve. This walkway could be in the form of a simple footpath. Another possibility is the construction of a boardwalk through the site. Boardwalks are excellent management tools for they provide non-degrading access which is essential in preserving the prairie's integrity while at the same time allowing the visiting public freedom to enjoy the prairie experience.

Finally, the area harbors an excellent seed source for use in local restoration projects. It also offers numerous opportunities for further scientific study on the dynamics of native American prairie. My research has only begun to scratch the surface. Other studies might include further botanical research, zoological studies, edaphic surveys, microbiological studies, historical and cultural studies, artistic expressions and others.

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APPENDIX A

An Explanation of the Index of Commonness

The Index of Commonness is a product of two values, frequency and cover, which allows species to be ranked according to their relative importance to a community. The frequency value reflects the proportion of quadrats in which a given species occurred in a sampled area. The cover value is a reflection of how much of each species was present in each quadrat, and is reported as an average figure. The product of the frequency and average cover values is called the Index of Commonness, and is directly related to the chances of finding a particular species at any given location in a community. This Index of Commonness has a maximum value of 10,000 where a species is found in all quadrats in large numbers, and a minimum value approaching zero for a rare plant found solitarily in only one quadrat (see Curtis 1959, Chapter 4 for a detailed discussion).

$$\text{Frequency} = \frac{\text{number of quadrats in which a species is present} \times 100}{\text{total number of quadrats}}$$

Cover = percentage of quadrat which a species represents

$$\text{Average Cover} = \frac{\text{sum of cover values for a particular species}}{\text{number of quadrats in which species is present}}$$

Index of Commonness = Frequency x Average Cover

FLORISTIC ANALYSIS OF PRAIRIE FENS IN THE SOUTHEASTERN MISSOURI OZARKS

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Abstract. A comprehensive inventory of four southeastern Missouri counties identified seven prairie fens ranging from 0.8 to 6.8 hectares in size on the Salem Plateau of the Ozark uplift. Missouri prairie fens represent the southernmost localities of a community type previously known only from north of the Wisconsinan glacial boundary. Unglaciated prairie fens occur in the deeply dissected, upper reaches of gaining stream valleys. A thick, weathered, cherty residuum of Cambrian-Ordovician dolomite overlies the uplands and acts as an unconsolidated aquifer. The vascular flora includes 243 taxa in 153 genera and 60 families. Approximately 41% belong to three families: Compositae (42), Cyperaceae (35), and Gramineae (24). These taxa belong to five floristic affiliations: midwestern tallgrass prairie 20%, wide ranging hydrophytic 29%, non-habitat-specific 37%, extraneous range disjunctions 8%, and seep-calciphiles 6%. Four microhabitats (gravelly marl, hydric-muck to mucky peat, mesic, and dry-mesic) corresponding to microtopographic variations are discussed and correlated with vegetational differences. Comparison of the prairie fen floras indicates that while there are species compositional differences, Missouri prairie fens are floristically similar to glaciated prairie fens.

INTRODUCTION

Prairie fens have been recognized in the literature from the Wisconsinan glaciated terrain of northeastern Illinois (Moran 1981), southeastern Wisconsin (Zimmerman 1978, 1983), southwestern Michigan (Kohring 1982), and west-central Ohio (Stuckey and Denny 1981). We define Missouri's prairie fens as a pyric-maintained natural community characterized by a caliciphilous flora locally dominated by mesic to wet-mesic prairie taxa on relatively firm, well decomposed, sapric mucky peat or mineral soil, constantly saturated by telluric, minerotrophic water at or just below the substrate surface. Although the term "prairie fen" is used, these fens occur in Missouri on unglaciated terrain outside the "prairie peninsula" (*sensu* Transeau 1935). The prairie fens of Missouri represent isolated southern localities of a natural community type previously thought restricted to glaciated regions.

Prairie fens, in contrast to mesic or wet-mesic midwestern tallgrass prairies, have a shallow histic epipedon overlying a mineral subsoil or somewhat "marly" calcareous substrate. Wet prairies, unlike prairie fens, are influenced by extreme fluctuations of the hydrologic regime (i.e., seasonal flooding, drought, etc.). Consequently, wet prairies do not provide a refugium for range disjunctions or fen calciphiles.

Natural features which distinguish prairie fens from calcareous seep-fens and sedge-shrub fens in southeastern Missouri are described by Orzell (1983). Calcareous seep-fens or marly fens are characterized by diffuse minerotrophic seepage from a shallow bedrock aquifer over grayish marly mineral soil (Lithic Haplaquepts) with parent material at or near the surface. Seep-fens occur in deeply dissected relatively small drainage basins, within the upper reaches of gaining streams on sideslopes in narrow valleys on slopes of 5-45%. A sparse to dense cover of cyperoid calciphiles (height < 30 cm) dominate marly flats, with medium-tall graminoids and mixed forbs on scattered tussock-formed mounds. Sedge-shrub or deep muck fens form on saturated histic soils (Typic Medisaprists) in moderately to deeply dissected terrain at the toeslopes of hills or bases of former valley terraces, on slopes of 0-5%. Dense cespitose bog-like mats (height 1.2-2.7 m) are dominated by cyperoids, mixed forbs, and scattered shrub thickets.

Missouri prairie fens occupy valley terraces of larger streams on slopes of 5-10%. Histic Humaquepts form in areas of copious seepage, whereas Typic Haplaquolls develop on less poorly drained microsites (Orzell 1983). Mixed tall graminoids and herbs (height 1.8-2.0 m) with high species richness characterize prairie fens.

Missouri fens had not been systematically botanized, although their flora was recognized as unique by Steyermark (1951a, 1951b, 1955, 1963), and documented in brief notes reporting plants from fens (i.e., calcareous wet meadows) as new additions to the Missouri flora (Steyermark 1938, 1949, 1952). This paper presents floristic data on unglaciated prairie fens in southeastern Missouri, a newly recognized natural community type in the state.

STUDY AREA

The study area is on the Salem Plateau of the south-central Ozark province, an unglaciated Paleozoic surface of dissected, karstified carbonate terrain (Fenneman 1938). Thom and Wilson (1980) characterize the region as the Lower Ozark Section of the Ozark Natural Division. Typical of the Salem Plateau is a thick mantle of weathered residuum derived from Upper Cambrian to Lower Ordovician aged cherty dolomites (Thacker and Anderson 1977, Wheeler 1965).

Missouri fens occur in the upper reaches of deeply dissected basins with a gaining stream where there is a thick weathered residuum overlying adjacent uplands and valley sideslopes. This permeable cherty mantle is presumed to be acting as an unconsolidated residuum aquifer (Aley 1968, 1978). Where groundwater is perched at the residuum-bedrock interface (along the upper reaches of gaining streams with sustained base flow) seepage-springs may form at toeslopes of stream terraces. These seepage-springs provide a constant flow of cold minerotrophic, telluric water to the fens.

Where prairie fens are known to occur in the northern United States they are found in glaciated terrain and are apparently not known from adjacent dissected unglaciated carbonate terrain. These glaciated prairie fens occur south of the "tension zone" (*sensu* Curtis 1959) in association with morainic deposits of coarse-textured outwash gravels. Northern Illinois prairie fens occur on slopes of morainal deposits, in morainal upland depressions, and on borders of postglacial lake beds or potholes (Moran 1981). Stuckey and Denny (1981) correlated Ohio prairie fens with porous calcareous gravel of esker-kame complexes with major end moraines. In Wisconsin, Zimmerman (1978, 1983) described prairie fens associated with porous calcareous Wisconsin-age glacial deposits overlying dissected Paleozoic dolomitic limestone and calcareous sandstone or with deep aquifers in Cambrian sandstone alongside preglacial valleys partly filled by glacial outwash.

The study area has a mid-continental, humid, mesothermal climate with warm summers and cool winters, with little or no water deficit in any season. The mean annual temperature at Goodland (Iron County), just north of the study area and in a topographic position similar to the prairie fens, is 13° C. Mean monthly temperatures normally range from 0° C in January to 24° C in July. There is an average of 169 frost-free days with the mean first fall freeze on October 2, and the mean last spring freeze on April 26. Mean annual precipitation is 108 cm, with

FIG. 1. Aerial view of 6.8 ha (16.8 acre) prairie fen (R61).

an average of 6 cm falling in February, the driest month, and 12 cm falling in April, the wettest month (USDA 1941). Average seasonal snowfall is 35 cm at Ironton, approximately 30 km east of Goodland.

METHODS

Inventory methods to locate prairie fens included examination of ASCS black and white aerial photographs in conjunction with 7.5' USGS topographic quadrangles, USDA-SCS soil surveys, and USGS geologic surveys. Hydrogeologic parameters, compilation of herbarium label data from former Steyermark "calcareous wet meadow" collection sites, literature sources, and interviews with local residents further refined the inventory. Valleys identified with potential for fens were screened from a single-engine, fixed-wing Cessna 210. Sites identified during the flight were marked on topographic maps to be field checked as potential prairie fens. Details of inventory methods are documented in Orzell (1983).

The vascular flora was documented by visiting each site twice monthly during each growing season from 1982 to 1983, with the exception of the Ripley and Howell county sites. Both of these sites were visited twice in the autumn of 1983 and once each in the spring of 1984. Voucher specimens were collected for deposit at the Missouri Botanical Garden in St. Louis. Based on field observations of more than 300 fens, geographic patterns for disjuncts, and habitat descriptions in Steyermark (1963), we recognized five general floristic affiliations in Missouri prairie fens. These may not necessarily represent range-wide habitat preferences. For example, seep-calciphiles may or may not be calciphiles outside the Ozark plateau.

Field observations of the physiognomic vegetational change in relation to hydrologic variations, microtopographic features, and edaphic factors allowed us to differentiate qualitatively four prairie fen microhabitats. Plant nomenclature follows Steyermark (1963). Specific legal locations for the study sites and voucher specimen data are available from the authors or the Missouri Department of Conservation.

RESULTS

Seven prairie fens ranging from 0.6 to 6.8 hectares were investigated in four southeastern Missouri counties (Carter-1, Howell-1, Ripley-1, Reynolds-4). Within these fens a total of 243 vascular plant taxa were vouchered, representing 60 plant families and 153 genera, with 18 (7%) introduced taxa (Table 1). The largest families were: Compositae, 42 taxa (17%), Cyperaceae, 35 taxa (14%), Gramineae, 24 taxa (10%), Rosaceae, 13 taxa (5%), and Leguminosae, 12 taxa (5%). Genera with the greatest number of taxa were *Carex*, 23 taxa (9%), *Panicum*, 8 taxa (3%), and *Juncus*, 7 taxa (3%).

These 243 taxa were then grouped into five floristic affiliations: midwestern tallgrass prairie taxa 49 (20%), wide ranging hydrophytic taxa 71 (29%), non-habitat-specific taxa 90 (37%), extraneous disjunct taxa 18 (7%), and seep-calciphiles 15 (6%) on the Ozark plateau.

Among the 49 prairie taxa, 18 (7% of total flora) are characteristic prairie plants; that is, these taxa display a high constancy to midwestern tallgrass prairies, and 31 (13%) are non-restrictive prairie plants. Some examples of characteristic prairie taxa encountered are *Andropogon gerardii, Castilleja coccinea,*

TABLE 1. Plant species of Missouri prairie fens: names of species preceded by an asterisk (*) are introduced species, (X^1) are restricted to grazed portion of site 1. Site 1 = R61 (R is county, 61 is reference number); Site 2 = R21E; Site 3 = R63A; Site 4 = RP1; Site 5 = C1; Site 6 = H4; Site 7 = R63E. Nomenclature follows Steyermark (1963) except for more recent nomenclature changes.

TAXA	1	2	3	4	5	6	7
*Achillea millefolium**	X						
Agalinis tenuifolia	X^1						
A. purpurea				X			
Agrimonia parviflora	X	X	X	X	X	X	
*Agrostis stolonifera**	X^1	X					
Ambrosia artemisiifolia var. *elatior*	X						
Amphicarpa bracteata	X			X			
Andropogon gerardii	X	X	X	X	X	X	
A. scoparius				X			
Anemone canadensis	X						
A. virginiana	X						
Apios americana	X	X	X	X			
Apocynum cannabinum	X						
Asclepias incarnata	X	X	X				X
A. tuberosa	X						
A. verticillata	X						
Ascyrum hypericoides	X						
Aster lateriflorus			X	X	X	X	
Aster novae-angliae	X	X		X	X	X	
A. pilosus	X^1						
A. praealtus	X	X				X	
A. puniceus var. *firmus* f. *lucidulus*	X	X	X				
*Barbarea vulgaris**	X^1						
Blephilia ciliata	X						
Boehmeria cylindrica	X		X	X		X	
Campanula aparinoides			X				
Cardamine bulbosa					X		
Carex bushii		X					
C. complanata var. *hirsuta*	X						
C. crinita							X
C. festucacea		X					
C. frankii	X						
C. granularis	X	X					
C. hystricina	X				X		
C. interior	X				X		
C. laevivaginata	X	X	X				
C. lanuginosa		X	X				
C. leptalea	X		X				
C. lupulina	X			X			
C. lurida	X	X	X	X	X		
C. meadii	X						
C. shortiana			X				
C. squarrosa	X						
C. stipata		X	X				
C. stricta var. *strictior*	X	X				X	
C. suberecta	X	X	X			X	
C. torta		X	X				
C. tribuloides			X				
C. trichocarpa	X	X					
C. vulpinoidea	X	X	X				
Cassia nictitans	X						
Castilleja coccinea	X			X	X		
Cephalanthus occidentalis		X	X	X	X	X	
Cercis canadensis	X						
Chelone glabra				X			
*Chrysanthemum leucanthemum**	X						
Cicuta maculata	X	X	X	X	X		X
Cirsium muticum	X				X		
Convolvulus sepium	X						
Coreopsis lanceolata	X						
C. pubescens					X		
C. tripteris	X			X		X	

Continued

TAXA	1	2	3	4	5	6	7
Cornus obliqua	X			X			
Crataegus crus-galli	X						
Cyperus strigosus	X			X			
Cypripedium calceolus var. *pubescens*					X		
Danthonia spicata	X						
*Daucus carota**	X						
Desmodium paniculatum	X						
*Dianthus armeria**	X						
Dioscorea villosa	X						
Diospyros virginiana	X						
Dulichium arundinaceum			X				
Echinochloa pungens	X[1]	X					
Eleocharis obtusa				X			
Elymus canadensis	X	X				X	
Erechtites hieracifolia	X						
Erigeron annuus	X[1]						
Eryngium yuccifolium					X	X	
Eupatorium coelestinum	X						
E. perfoliatum		X	X	X			
Euphorbia corollata	X						
*Festuca elatior**	X[1]	X					
Filipendula rubra		X	X			X	
Fimbristylis caroliniana	X						
Fragaria virginiana	X			X			
Fraxinus pennsylvanica	X						
Fuirena simplex				X		X	
Galium obtusum		X					
G. triflorum	X						
Gaura biennis	X						
Gentiana quinquefolia var. *occidentalis*	X						
Geum canadense	X	X	X				
Gleditsia triacanthos	X						
Glyceria striata	X	X	X				X
Helenium autumnale	X	X		X	X	X	
Helianthus grosseserratus	X						
H. maximiliana					X		
H. mollis	X					X	
Houstonia longifolia	X						
H. pusilla	X						
Hypericum mutilum	X						
H. punctatum	X						
H. spathulatum	X						
Hypoxis hirsuta					X		
Ilex decidua				X			
Impatiens capensis			X	X			
Juncus brachycarpus				X			
J. dudleyi	X						
J. effusus var. *solutus*	X	X	X				X
J. interior				X			
J. subcaudatus	X			X			
J. tenuis		X	X				
J. torreyi						X	
Juniperus virginiana	X						
Lactuca canadensis	X						
Lathyrus palustris	X	X					
Leersia oryzoides		X	X				
*Lepidium campestre**	X						
Lespedeza procumbens	X						
Liatris pycnostachya					X		
Lilium michiganense	X						
Linum medium var. *texanum*	X			X			
L. striatum	X						
Liparis loeselii					X		
Lobelia cardinalis	X						
L. inflata	X						
L. siphilitica	X			X	X		
Ludwigia alternifolia	X	X	X	X	X		
L. microcarpa				X			
L. palustris	X[1]						

Continued

TAXA	1	2	3	4	5	6	7
Lycopus americanus	X		X	X			
Lysimachia quadriflora	X	X		X	X	X	X
Lythrum alatum	X	X	X	X	X	X	X
Melanthium virginicum			X				
Mentha x *piperita*			X				
Mimulus ringens	X	X			X	X	X
Monarda fistulosa	X						
*Nasturtium officinale**		X					
Nuphar luteum		X					
Onoclea sensibilis	X	X	X				
Osmunda regalis var. *spectabilis*	X		X	X			
Oxalis stricta	X						
Oxypolis rigidior	X	X		X	X	X	X
Panicum anceps	X			X	X		
P. clandestinum	X		X				
P. flexile	X						
P. lanuginosum	X						
P. microcarpon	X			X			
P. oligosanthes	X						
P. scoparium				X			
P. sphaerocarpon	X			X			
Parnassia grandifolia	X			X		X	
Parthenium intergrifolium	X						
Pedicularis lanceolata	X		X	X	X	X	
Penstemon digitalis	X	X	X		X		
Phacelia gilioides	X						
*Phleum pratense**	X	X	X				X
Phlox glaberrima				X			
P. maculata var. *pyramidalis*		X			X		
P. pilosa	X						
Physocarpus opulifolius	X			X	X		
Physostegia angustifolia				X			
P. virginiana	X			X			
Pinus echinata	X			X			
*Plantago lanceolata**	X[1]						
Platanthera lacera	X						
P. leucophaea (historical)					X		
Platanus occidentalis	X	X					
Poa compressa	X[1]						
P. pratensis		X					
Polygonum hydropiperoides				X			
P. sagattatum		X		X			
*Potentilla recta**	X						
P. simplex	X			X			
Prunella vulgaris var. *lanceolata*	X			X			
Prunus americana	X						
P. serotina	X						
Psoralea onobrychis	X						
P. psoralioides var. *eglandulosa*	X		X		X		
Ptilimnium nuttallii	X						
Pycnanthemum tenuifolium	X	X	X	X			
P. virginianum	X	X	X		X	X	X
Quercus alba				X			
Ranunculus septentrionalis					X		
Ratibida pinnata	X						
Rhus copallina var. *latifolia*	X			X			
R. radicans	X						
Rhynchospora capillacea						X	
R. capitellata	X			X	X		
*Rosa multiflora**	X						
R. setigera	X						
Rubus flagellaris	X						
Rudbeckia fulgida var. *umbrosa*	X	X	X	X	X	X	X
R. hirta	X						
R. missouriensis	X				X		
R. subtomentosa	X		X				
R. triloba	X						
Ruellia humilis					X		

Continued

TAXA	1	2	3	4	5	6	7
Sabatia angularis	X						
Sagittaria latifolia		X					
Salix caroliniana	X		X				
S. rigida	X		X	X			
S. sericea	X		X	X	X		
Salvia lyrata				X	X		
Satureja arkansana				X			
Scirpus americanus				X			
S. atrovirens	X	X	X	X	X		X
S. lineatus (S. pendulus)	X	X	X			X	X
S. validus		X	X	X		X	
Scleria verticillata	X			X	X		
Scutellaria elliptica	X						
Senecio aureus	X		X	X	X		
Silphium integrifolium	X	X	X	X			
S. perfoliatum	X						
S. terebinthinaceum	X				X	X	
Sisyrinchium campestre	X						
Solidago altissima	X	X				X	
S. nemoralis	X						
S. patula var. *patula*	X			X			
S. riddellii	X			X			
S. rigida					X		
S. rugosa			X				
Sorghastrum nutans				X	X		
Sparganium americanum		X					
Spartina pectinata	X	X					
Spiranthes cernua	X						
Symphoricarpos orbiculatus	X						
Thalictrum revolutum	X				X		
Thelypteris palustris var. *pubescens*	X	X	X				
Tridens flavus	X[1]						
*Trifolium campestre**	X[1]						
*T. pratense**	X[1]						
Tripsacum dactyloides	X						
Typha latifolia						X	
Ulmus rubra	X			X			
Vernonia baldwinii	X	X	X				
V. crinita						X	
V. missurica	X						
Veronicastrum virginicum	X	X	X		X	X	X
Viola cacullata			X				
Vitis aestivalis	X						
Xyris torta				X			

Coreopsis tripteris, Elymus canadensis, Lathyrus palustris, Rudbeckia subtomentosa, Spartina pectinata, and *Veronicastrum virginicum*. Non-restrictive prairie plants include *Anemone canadensis, Asclepias tuberosa, Carex meadii, Helianthus mollis, Hypoxis hirsuta, Parthenium integrifolium, Phlox pilosa, Ratibida pinnata*, and *Ruellia humilis*.

Hydrophytic or wetland plants comprise 71 taxa, including *Boehmeria cylindrica, Carex crinita, C. lupulina, C. vulpinoidea, Cephalanthus occidentalis, Dulichium arundinaceum*, and *Eupatorium perfoliatum*.

The 90 non-habitat-specific plants include 18 (7%) introduced taxa (Table 1), 7 (3%) native, nonpersisting accidentals, and 65 (27%) wide-ranging indigenous taxa with broad ecological amplitudes. Examples of native, nonpersisting accidentals in fens include *Pinus echinata, Ilex decidua, Quercus alba, Rhus copallina* var. *latifolia, R. radicans*, and *Ulmus rubra*. Wide ranging taxa included *Silphium perfoliatum, Apocynum cannabinum, Danthonia spicata, Dioscorea villosa, Houstonia pusilla, Hypericum punctatum*, and *Scutellaria elliptica*.

Eighteen extraneous taxa and 15 Ozark plateau seep-calciphiles comprise 14% of the flora. Extraneous taxa (Table 2) display range disjunctions to the Salem Plateau of southeast Missouri and occasionally into adjacent northeastern Arkansas. All the extraneous taxa with the exception of *Xyris torta* can also be considered seep-calciphiles on the Salem Plateau. These taxa are primarily "near-modal" (*sensu* Curtis 1959) fen plants where they occur on the Salem Plateau. Eight of the extraneous taxa are either rare or endangered in Missouri (Wilson 1984). Five prairie fen plants are listed as state endangered (*Campanula aparinoides, Xyris torta, Liparis loeselii, Filipendula rubra*, and *Ludwigia microcarpa*) and three as state rare (*Carex stricta, C. trichocarpa*, and *Phlox maculata* var. *pyramidalis*). Seep-calciphiles frequently are indicators of fens on the Salem Plateau but can also occur in similar calcareous habitats (i.e., along spring branches or spring-fed streamsides, bluff seeps, or seeps on calcareous glades). Ozark plateau seep-calciphiles not displaying a disjunct distribution pattern are *Aster praealtus, Cardamine bulbosa, Carex granularis, C. hystricina, C. laevivaginata, C. lanuginosa, C. leptalea, Fuirena simplex, Lysimachia quadriflora, Panicum flexile, Parnassia grandifolia, Pycnanthemum virginianum, Rudbeckia fulgida* var. *umbrosa, Salix sericea*, and *Viola cucullata*.

We recognize four prairie fen microhabitats in Missouri which correspond to microtopographic, edaphic, and hydrologic variations. These are gravelly marl, hydric-muck to mucky peat, mesic, and

dry-mesic areas. Different prairie fen microhabitats support vegetation of rather distinct physiognomy and high beta species diversity, and are found in a complex pattern within each site. The result is a mixture of prairie, calciphilic, and hydrophytic plant species at each site, which is characteristic of the prairie fen community type.

Discharge of diffuse cold, circumneutral, minerotrophic groundwater can either produce exposed patches of gravelly calcareous matrix or hydric mucky peat. The gravelly marl areas are dominated by cyperoids such as *Carex hystricina, Fuirena simplex, Rhynchospora capillacea*, and *Scleria verticillata* less than 30 cm tall, with *Satureja arkansana* and *Parnassia grandifolia*. Soil moisture varies with seasonal water table fluctuations, evapotranspiration rates, etc.; under dry summer weather conditions, free surface water may evaporate, but the marly ooze remains moist. Copious seepage may form seep-spring rivulets with *Nuphar luteum, Carex torta*, and *C. hystricina*, bordered with *Senecio aureus, Parnassia grandifolia, Cardamine bulbosa, Fuirena simplex*, and *Rudbeckia fulgida* var. *umbrosa*. Drier elevated hummocks in marly areas are often dominated by *Andropogon gerardii* or *Sorghastrum nutans*, with *Rudbeckia missouriensis, Liatris pycnostachya*, and mixed prairie forbs.

Organic muck or mucky peat with uniform internal seepage, forming in discharge depressions, is characterized by cespitose sedges, wetland forbs, calciphiles, mat-forming mosses and low-growing shrubs. Frequent species include *Solidago patula* var. *patula, Scirpus atrovirens, Rudbeckia fulgida* var. *umbrosa, Senecio aureus, Parnassia grandifolia, Carex leptalea, Lysimachia quadriflora*, and occasionally *Solidago riddellii, Cirsium muticum, Chelone glabra*, and *Carex stricta*. Poor internal drainage may result in shallow ephemeral pools, where typical hydrophytes like *Asclepias incarnata, Cephalanthus occidentalis*, and species of *Juncus, Eleocharis*, and *Polygonum* are conspicuous components. Slightly better drained organic substrates support *Aster novae-angliae, A. puniceus, Lythrum alatum, Eupatorium perfoliatum, Phlox maculata* var. *pyramidalis, Pedicularis lanceolata, Oxypolis rigidior, Viola cucullata, Carex lanuginosa, C. lurida, Lobelia siphilitica, Mimulus ringens, Scirpus lineatus*, and *Vernonia baldwinii*. Scattered low shrubs such as *Cornus obliqua, Physocarpus obtusifolius*, and *Salix sericea* are sometimes present.

Mineral soils of prairie fens on slightly elevated, less poorly drained microhabitats are most prone to seasonal water table fluctuations. Mottling of the subsoil indicated fluctuations between aerobic and anaerobic conditions, as viewed in soil pits at some sites. Because of the better aeration of these soils, organic matter is incorporated into the mull layer, rather than accumulated as muck. These mesic microhabitats are dominated by dense stands (height 1.8-2.0 m) of graminoids and prairie forbs. Dominants include *Andropogon gerardii* and *Spartina pectinata*, with *Veronicastrum virginicum, Lilium michiganense, Aster praealtus, Pycnanthemum virginianum, Thalictrum revolutum*, and rarely *Carex stricta*.

Growth and litter decomposition by the graminoid cover results in raising the microhabitat farther above the water table, favoring dry-mesic adapted mixed forbs including *Asclepias tuberosa, Carex complanata* var. *hirsuta, Castilleja coccinea, Euphorbia corollata, Eryngium yuccifolium, Helianthus mollis, Hypericum spathulatum, Coreopsis tripteris, Sabatia angularis, Silphium terebinthinaceum, S. integrifolium, Rudbeckia hirta, R. subtomentosa, Ruellia humilis, Spiranthes cernua, Scirpus lineatus*, and *Pycnanthemum tenuifolium*.

DISCUSSION

The total vascular flora of Missouri prairie fens is quite similar to that described for fens in other regions. Curtis (1959) found that the largest families in six Wisconsin fens were Asteraceae (17.4%), Poaceae (8.7%), Lamiaceae (5.2%), Cyperaceae (4.3%), Apiaceae (4.3%), Scrophulariaceae (4.3%), Salicaceae (3.5%), and Rosaceae (3.5%). The seven largest families from a Michigan prairie fen were Poaceae (21.7%), Asteraceae (16.5%), Cyperaceae (8.0%), Liliaceae (2.3%), Lamiaceae (2.3%), Scrophulariaceae (1.7%), and Juncaceae (1.7%) (Kohring 1982). As calculated from data in Zimmerman (1983), Asteraceae (14.7%), Cyperaceae (25.2%), Poaceae (9.4%), and Salicaceae (8.4%) are the largest families in a Wisconsin prairie fen. Holte (1966) noted the largest families from a fen complex in northwestern Iowa as Asteraceae (19.3%), Poaceae (11.7%), and Cyperaceae (11.7%). Comparison of our floristic list with those from other prairie fens is limited because most studies only list the prevalent species.

Various floristic analyses of glaciated prairie fens have been published (Zimmerman 1983, Stuckey and Denny 1981, Moran 1981). Zimmerman (1983) considered the floristic affiliations of a Wisconsin prairie fen to be prairie grassland (10%), general wetland (48%), bog (7%), and wet calcicoles (35%). Based on geographic affinities Stuckey and Denny (1981) determined that 74 distinctive species of Ohio fens include four floristic elements: northeastern (41%), northwestern (26%), southeastern (28%), and 5% other taxa. Southeastern taxa were best represented from west-central Ohio prairie fens and are also characteristic of wet prairies (Stuckey and Denny 1981). Moran (1981) noted that northern Illinois prairie fens support calciphilic taxa, typical mesic and wet-mesic prairie taxa, marsh taxa, and boreal relict taxa. Prairie, hydrophytic, and calciphilic taxa noted in the above studies are similar to those of Missouri prairie fens.

Andropogon gerardii, a characteristic prairie grass, is present in the prairie fens of Ohio (Stuckey and Denny 1981) and Wisconsin (Zimmerman 1983), and dominant in Illinois prairie fens (Moran 1981). *Andropogon scoparius*, a codominant with *A. gerardii* in Illinois prairie fens (Moran 1981), and also present in Ohio prairie fens (Stuckey and Denny 1981), is much less frequent in Missouri prairie fens. *Sorghastrum nutans* and *Spartina pectinata*, both conspicuous in Missouri prairie fens, are also listed for Ohio and Illinois (Foos 1971, Stuckey and Denny 1981, Moran 1981) and Wisconsin (Zimmerman 1983, Curtis 1959) respectively.

The disjunct or relictual component of the fen flora is also consistent with those recognized by others (Anderson 1943, Bartgis and Lang 1984, Conard 1952, Curtis 1959, Foos 1971, Frederick 1974a, 1974b, Friesner and Potzger 1946, Hayden 1943, Hutton et al. 1968, McLeod 1983a, Moran 1981, Ogle 1982, Reimer 1962, Starcs 1962, Stuckey and Denny 1981, Tucker 1972, Zimmerman 1978, 1983). All of the disjunct taxa (except for *Juncus subcaudatus* and *Ludwigia microcarpa*) in Missouri prairie fens are often found in northern fens and prairie fens. Some of the Missouri prairie fen disjunct taxa with northern, northeastern, and north-central geographic affinities (Table 2) display an isolated secondary concentration of records on the Ozark plateau (Orzell et al. 1985). Apparently, continuous saturation of the mucky peat substrate by cold, telluric, minerotrophic water has allowed northern disjunct taxa to survive in Missouri prairie fens since Pleistocene glaciation.

Numerous northern near-modal fen taxa including *Parnassia glauca, Lobelia kalmii, Solidago ohioensis, Potentilla fruticosa, Aster junciformis*, and *Gentianopsis procera* are primarily confined to glaciated territory, and absent from Missouri prairie fens. In addition, carnivorous "bog" taxa (*Sarracenia purpurea, Drosera* spp., *Utricularia* spp.) most frequent in ombrotrophic wetlands and also noted from a Wisconsin prairie fen (Zimmerman 1983), Ohio bog-fens (Stuckey and Denny 1981), North Carolina bog-fens (McLeod 1983b, Tucker 1972) and southwestern Virginia fens (Ogle 1982) are conspicuously lacking from Missouri prairie fens.

Seep-calciphiles and extraneous taxa which are obligate Ozark calciphiles often frequent fen and other calcareous habitats (alkaline meadows, pannes, etc.) where they occur north of the Wisconsinan glacial boundary and south of the "tension zone" (*sensu* Curtis 1959). These include *Lysimachia quadriflora* (Iltis and Shaughnessy 1960, Iltis 1965), *Scleria verticillata* (Smith 1983), *Carex interior* (Wheeler and Ownbey 1984, Reznicek and Ball 1980), and

TABLE 2. Geographic affinities of extraneous Missouri prairie fen taxa.

Taxon	Geographic Affinity
Aster puniceus var. *firmus* f. *lucidulus*	northeastern
Campanula aparinoides	northeastern
Carex interior	northern
Carex stricta var. *strictior*	northeastern
Carex suberecta	north-central
Carex trichocarpa	northeastern
Cirsium muticum	northeastern
Filipendula rubra	north-central
Juncus subcaudatus	eastern
Liparis loeselii	northeastern
Ludwigia microcarpa	southeastern
Pedicularis lanceolata	northeastern
Phlox maculata var. *pyramidalis*	eastern
Rhynchospora capillacea	northern
Scleria verticillata	southern
Solidago patula var. *patula*	northeastern
Solidago riddellii	north-central
Xyris torta	southern

Rhynchospora capillacea (Seischab and Bernard 1985, Smith 1983, Lammers and van der Valk 1979). In conclusion, despite numerous species compositional differences, Missouri prairie fens are quite similar to northern prairie fens in both floristic spectra and components.

Numerous fen studies (Collins et al. 1982, Foos 1971, Holte 1966, McLeod 1983b, Schwintzer 1978, Sims et al. 1982, Slack et al. 1980, Stuckey and Denny 1981, Sytsma and Pippen 1982, van der Valk 1975, 1976, among others) have demonstrated that vegetational gradients correspond to fen microtopography, hydrology, and edaphic variations. Although regional floristics vary, the overall similarity of the physiognomy of vegetation gradients between Missouri prairie fens and these studies suggests that similar environmental gradients and vegetation responses exist in fen environments.

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FLORA OF LIME LAKE FEN SPRING ARBOR, MICHIGAN

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Abstract. Extensive extraction of marl from a marshy area southeast of Spring Arbor, Michigan at the beginning of the century created Lime Lake. Undisturbed in the years following 1929, when marl production was discontinued, a fen community gradually developed along the southeastern shore of Lime Lake. A recent floristic study of the fen revealed more than 130 species of vascular plants. Composites, with 35 species, represent the largest family, whereas, sedges are represented by 20 species and grasses by 16 species.

Of Curtis' 41 prevalent species for Wisconsin fens, 36 occur at the Lime Lake fen and of 36 typical fen species listed for northeastern Illinois by Moran, 32 grow on the study tract, confirming the fact that its composition is similar to other fens of the western Great Lakes region.

Sporobolus heterolepis, a species on the Michigan list of endangered plants, is of common occurrence on this fen.

INTRODUCTION

Lime Lake fen is located at the southeastern edge of Lime Lake in the NE 1/4 of section 28 of Spring Arbor Township (T3S-R2W), Jackson County, Michigan, 3 kilometers southeast of Spring Arbor village. At the beginning of the century this area was extensively mined for marl, first by the Pyramid Portland Cement Company. It planned to mine 1,200 bbl. of marl per day based on a report by the Douglass Houghton Survey (Hale 1903) which stated that "the town of Spring Arbor abounds in extensive beds of marl." Later, operations were taken over by the Peerless Portland Cement Company (Spring Arbor Historical Society 1980) and marl was dredged from this area until 1929 when operations were discontinued because marl costs were much higher than that of plants using rock lime. The extent of marl operations at Lime Lake, however, is apparent by comparing the large lake which now exists at this location with only a marsh shown in this area on early maps (Interstate 1881).

Fifty years have passed since the dredging of marl at this location. The study tract now consists of several large open areas dominated by species which appear to be typical of a fen, compared to fens found in southern Michigan (Thompson 1983). These openings are enclosed by narrow bands of shrubs consisting principally of gray, red-osier, and silky dogwoods, and several shrubby willows. Of interest is a small stream that forms the southern border of the fen. The stream is formed by a large, bubbling spring that rises a short distance to the south, then flows northward almost

TABLE 1. Fen border plants and edge invaders.

Juniperus virginiana	red cedar
Populus tremuloides	quaking aspen
Salix bebbiana	Bebb willow
S. candida	hoary willow
S. glaucophyloides	glaucous willow
S. interior	sandbar willow
Betula pumila	bog birch
Corylus americana	hazelnut
Amelanchier sanguinea	roundleaf shadbush
Crataegus spp.	hawthorn
Physocarpus opulifolius	ninebark
Prunus virginiana	chokecherry
Zanthoxylum americanum	prickly ash
Rhus glabra	smooth sumac
Acer rubrum	red maple
Rhamnus alnifolius	bog buckthorn
R. frangula	glossy buckthorn
Cornus purpusi	silky dogwood
C. racemosa	gray dogwood
C. stolonifera	red-osier dogwood
Fraxinus nigra	black ash
Lonicera dioica	vine honeysuckle
Viburnum lentago	nannyberry
V. trilobum	highbush cranberry

TABLE 2. Floristic composition of Lime Lake Fen.

Composites (Compositae)	
Aster azureus	azure aster
A. novae-angliae	New England aster
A. puniceus	redstem aster
A. lucidulus	glossyleaf aster
A. laevis	smooth aster
A. junciformis	bog aster
A. umbellatus	flat-top aster
A. cordifolius	heartleaf aster
A. pilosus	hairy aster
A. laterifolius	calico aster
A. simplex	panicle aster
A. faxoni	faxon aster
Cirsium muticum	swamp thistle
Erigeron strigosus	narrowleaf fleabane
Eupatorium maculatum	Joe-pyeweed
E. perfoliatum	boneset
Helianthus giganteus	giant sunflower
H. grosse serratus	largetooth sunflower
Liatris spicata	spiked blazing star
Prenanthes racemosa	white lettuce
Ratibida pinnata	prairie coneflower
Rudbeckia hirta	black-eyed susan
R. fulgida	showy coneflower
Senecio aureus	golden ragwort
S. pauperculus	prairie ragwort
Silphium terebinthinaceum	prairie dock
Solidago juncea	early goldenrod
S. uliginosa	bog goldenrod
S. nemoralis	gray goldenrod
S. gigantea	giant goldenrod
S. canadensis	Canada goldenrod
S. altissama	tall goldenrod
S. ohioensis	Ohio goldenrod
S. riddellii	Riddell goldenrod
S. graminifolia	grassleaf goldenrod
Grasses (Gramineae)	
Andropogen gerardii	big bluestem
A. scoparius	little bluestem
Bromus ciliatus	fringed brome
B. kalmii	prairie brome
Calamagrostis canadensis	bluejoint
Festuca arundinacea	tall fescue
Glyceria striata	manna grass
Panicum flexile	wiry panic grass
P. lindheimeri	Lindheimer panic grass
Phragmites communis	reedgrass
Poa compressa	Canada bluegrass
Spartina pectinata	prairie cordgrass
Sporobolus heterolepis	prairie dropseed
S. vaginiflorus	sheathed dropseed
Sorghastrum nutans	Indiangrass
Sedges (Cyperaceae)	
C. aquatilis	water sedge
C. aurea	goldfruit sedge
C. buxbaumii	Buxbaum sedge
C. crawei	Crawe sedge
C. hystericina	bottlebrush sedge
C. lasiocarpa	slender sedge
C. leptalea	delicate sedge
C. lurida	shiny sedge
C. scoparia	broom sedge
C. sterilis	prickly sedge
C. stricta	tussock sedge
C. tetanica	wood sedge
C. viridula	greenish sedge
Cyperus rivularis	river sedge
Eleocharis spp.	spikerush
Juncus dudleyi	Dudley rush
Scirpus americanus	three-square
S. atrovirens	green bulrush
S. cyperinus	wool grass
Mints (Labiatae)	
Blephilia ciliata	woodmint
Lycopus americanus	cutleaf horehound
Mentha piperata	peppermint
Monarda fistulosa	wild bergamot
Prunella vulgaris	self-heal
Pycnanthemum virginianum	mountain mint
Roses (Rosaceae)	
Agrimonia grygosepala	agrimony
Fragaria virginiana	wild strawberry
Pontentilla canadensis	creeping cinquefoil
P. fruticosa	shrubby cinquefoil
Rosa palustris	swamp rose
Umbels (Umbelliferae)	
Cicuta maculata	water hemlock
Daucus carota	wild carrot
Oxypolis rigidior	cowbane
Pastinacea sativa	wild parsnip
Zizia aurea	golden alexanders
Violets (Violaceae)	
Viola affinis	Le Conte violet
V. cucullata	bog violet
V. rostata	longspur violet
V. septentrionalis	northern blue violet
V. sororia	wooly blue violet
Legumes (Fabaceae)	
Lathyrus palustris	marsh pea
Lespedezea capitata	narrowleaf bush clover
Lupinus perennis	lupine
Melilotus alba	white sweet clover
Lillies (Liliaceae)	
Lilium michiganense	Michigan lily
Smilacina stellata	starry false Solomon seal
Tofieldia glutinosa	false asphodel
Zygadenus glaucus	white camass
Additional species	
Equisetum arvense	field horsetail
Thelypteris palustris	marsh fern
Typha latifolia	common cattail
Triglochin palustre	marsh arrowgrass
Arisaema triphyllum	jack-in-the-pulpit
Symplocarpus foetidus	skunk cabbage
Tradescantia ohiensis	spiderwort
Dioscorea villosa	wild yam
Hypoxis hirsuta	yellow stargrass
Iris shrevei	south blue iris
Sisyrinchium albidum	white blue-eyed grass
Cypripedium calceolus	yellow ladyslipper
Spiranthes cernua	nodding ladies tresses
Saponaria officinalis	soapwort
Comandra richardsiana	false toadflax
Rumex crispus	curly dock
Anemone virginiana	thimbleweed
Caltha palustris	marsh marigold
Thalictrum dasycarpum	tall meadow rue
Parnassia glauca	grass of parnassus
Euphorbia corollata	flowering spurge
Impatiens biflora	jewelweed
Parthenocissus quinquefolia	Virginia creeper
Vitis riparia	wild grape
Lythrum salicaria	showy lythrum
Steironema quadriflorum	narrowleaf loosestrife
Gentiana andrewsii	bottled gentian
G. procera	fringed gentian
Apocynum sibiricum	sessile Indian hemp
Asclepias incarnata	swamp milkweed
A. tuberosa	orange milkweed
Convolvulus sepium	hedge bindweed
Lithospermum canescens	hoary puccoon
Physalis heterophylla	clammy ground cherry
Gerardia purpurea	purple gerardia
Pedicularis lanceolata	swamp betony
Utricularia cornuta	horned bladderwort
Galium boreale	northern bedstraw
Echincocystis lobata	wild cucumber
Campanula aparinoides	marsh bellflower
Lobelia kalmii	kalm lobelia
L. siphilitica	giant lobelia
L. spicata	pale spike lobelia

parallel to the shore of Lime Lake before it turns eastward and runs into a small lake nearby. The soil at the fen area is classed as Martisco soil which consists of poorly drained decomposed herbaceous material laid down over marl. The pH ranges from 7.6 to 8.0.

In view of the past history of the tract the authors concluded that it would be of interest to study its flora and to determine its vegetational character.

PROCEDURE AND METHODS

Survey trips were made to the Lime Lake fen in spring, early and late summer, and early fall during the years 1982-84 to catalog the plants growing there. Specimens of the more interesting species were collected and incorporated into the herbarium at Spring Arbor College or the Billington Herbarium at Cranbrook Institute of Science, located in Bloomfield Hills, Michigan. Plants were identified according to the nomenclature used in Gleason's Britton and Brown (1952).

The plants found in the fen are listed in Tables 1 and 2. Families represented by four or more species are tabulated in numerical order, beginning with the largest family. The balance of the plants, listed as Additional species, were arranged in the order (phylogenetic) shown in Gleason's Britton and Brown. The common names used are principally those of Hall and Thompson (1959).

RESULTS AND CONCLUSIONS

The list of plants inhabiting the Lime Lake fen, presented in Table 2, includes more than 130 species of vascular plants. The composite family (Compositae) with 35 species is the largest. With 20 species the sedges (Cyperaceae) and the grasses (Gramineae) with 16 species rank second and third, respectively. Families represented by 5 or 6 species each are mints (Labiatae), roses (Rosaceae), umbels (Umbelliferae), and violets (Violaceae). Legumes (Fabaceae) and lilies (Liliaceae) total 4 species each.

Conspicuous plants in the spring season are: golden alexanders, hoary puccoon, marsh fern, narrowleaf loosestrife, prairie ragwort, shrubby cinquefoil, and wild strawberry. Prominent species during the early summer include: Buxbaum sedge, cowbane, Crawe sedge, Dudley rush, swamp milkweed, swamp thistle, woodmint, and prairie dropseed which is on the Michigan list of rare, threatened, and endangered plants. Dominant plants of late summer include big bluestem grass, bog goldenrod, grass-of-Parnassus, Indian grass, New England aster, Ohio goldenrod, Riddell goldenrod, and smooth aster. Kalm lobelia, marsh arrowgrass, and tussock sedge are located along the stream area.

To determine the vegetative character of the tract the species composition was compared with the list of prevalent species of Wisconsin fens (Curtis 1959) and of fens of northern Illinois (Moran 1981). Of the Curtis list of 41 fen species for Wisconsin, 36 occur on the Lime Lake tract and of Moran's list of 36 fen species, 32 are found in this area. It is concluded that the Lime Lake area has a composition similar to that of other fens in the western Great Lakes region and, although the area was greatly disturbed in the past, it has now developed into an excellent fen community.

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DISTRIBUTION OF BRYOPHYTES IN SELECTED WESTERN MISSOURI AND WESTERN ARKANSAS PRAIRIES

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Abstract. A bryological study of prairies in western Missouri and western Arkansas was conducted between fall 1982 and spring 1984, in order to gain further understanding of species distribution in midwest prairies. Collections resulted in a total of 30 taxa representing 2 classes and 20 families. Twenty-one taxa are terrestrial while the remaining are corticolous (on wood). *Weissia controversa* Hedw. was found on all prairies surveyed while *Campylium hispidulum* (Brid.) Mitt. and *Amblystegium varium* (Hedw.) Lindb. were found on all but one prairie each. The remaining taxa were sporadically collected from the prairies studied.

INTRODUCTION

Limited information on the distribution of bryophytes in tallgrass prairies of the midwestern United States is available and most of that known is the result of past bryofloristic surveys (Hague 1930, Sharp 1930, Conard 1945, Hatcher 1952, Gier 1955, McGregor 1950, Smith 1966, Zales 1971, McCleary and Redfearn 1979, Redfearn 1972), which did not concentrate directly on collecting from among prairie grasses and forbs. A few bryoecological studies have given attention to the tallgrass prairie and have provided species lists. Duncan (1959) reported 51 taxa from 23 counties in eastern Kansas. Timme (1983) reported 9 taxa for a small prairie in southwest Missouri and O'Keefe van der Linden and Farrar (1983) reported 34 taxa for a prairie in northwest Iowa.

The factors affecting the success of prairie bryophytes have received some recent attention. Certainly, vegetational, topographic, and climatic factors will have important effects on their success. Lee and Stewart (1971) suggested that drought resistance in mosses results from a physiological response rather than morphological attributes. It is thought also that for some species the cytoplasm is highly desiccation tolerant (Hinshiri and Proctor 1971). This phenomena has been studied by several workers (Bewley 1973, 1979, Stewart and Lee 1972, Tucker et al. 1975, Dhinsda and Bewley 1976, 1977, 1978, Krochko et al. 1979.)

O'Keefe van der Linden and Farrar (1983) suggested that the growth form of a species may result in differences in distribution on a prairie in northwest Iowa. Results from their study indicated that pleurocarpous (''prostrate'') mosses as a group were restricted to the northeast-facing slopes where evaporation and surface temperatures were significantly lower than those of southwest-facing slopes. Acrocarpous (''upright'') species were more abundant on southwest-facing slopes. Timme (1983) found the pleurocarpous moss *Campylium hispidulum* Mitt. to be the most abundant moss in a small prairie in southwest Missouri. This prairie is relatively level with a southwest-facing knoll in the eastern part, where *C. hispidulum* Mitt. also occurred. Another moss, *Byroandersonia illecebra* (Hedw.) Robins., was found as extensive mats only in the western one-third of the prairie. More studies are needed in order to determine if a relationship exists between the growth forms of bryophytes and the topography of prairies.

The purpose of this study was to investigate the distribution of bryophytes in tallgrass prairies of western Missouri and western Arkansas. The study is a continuation and expansion of an earlier study (Timme 1983) of bryophytes of a tallgrass prairie in southwestern Missouri. These results, and results from future studies, will be used to obtain a better understanding of the bryogeography of tallgrass prairies of the midwestern United States.

DESCRIPTION OF STUDY AREAS

Fig. 1 shows the location of the 12 prairies surveyed. These prairies extend from approximately 38.5° latitude, 94.5° longitude to approximately 34.5° latitude, 94.5° longitude. They are located in the westernmost counties of Missouri and Arkansas.

The bedrock is of Mississippian and Pennsylvanian age (Oeting et al. 1966). Dorsett Hill prairie, the northernmost prairie surveyed, is Missourian series limestone of Pennsylvanian age. Golden, Pawhuska, Catlin, Osage, Massard, and Witcherville prairies are Desmoinesian series limestone, shale, and sandstone of Pennsylvanian age. Mount Vernon, Penn-Sylvania, and Diamond prairies are Kinderhookian and Osagean series limestone (mixed with chert), shale and sandstone of Mississippian age. Stump prairie is Chesterian and Morrowan series limestone, shale and sandstone of late Mississippian early Pennsylvanian age. Mena prairie, the southernmost prairie surveyed, is Meramecian series limestone of Mississippian age. All the prairies are considered to be of the upland type with silt loam soils derived from sandstone, limestone and shale or some combination thereof (Crow 1974, Toney 1978). All the prairies occur on unglaciated terrain.

FIG. 1. Location of prairies. Missouri: DH = Dorsett Hill, Cass Co.; OS = Osage, Vernon Co.; PA = Pawhuska, CA - Catlin, and GO = Golden, Barton Co.; PS = Penn-Sylvania, Dade Co.; MV = Mount Vernon, Lawrence Co.; DI = Diamond, Newton Co.; Arkansas: ST = Stump, Benton Co.; MA = Massard and WI = Witcherville, Sebastian Co.; ME = Mena, Polk Co.

Fig. 2 shows the climatic divisions with mean annual precipitation for the areas in which the prairies surveyed are located (National Oceanic and Atmospheric Administration 1983). There is a 261 mm increase in amount of annual precipitation between the west central plains of Missouri and west central Arkansas. No significant difference exists for mean monthly total precipitation.

Normal average daily temperatures differ by 10° between the west central plains of Missouri and west central Arkansas early in the year. The temperatures tend to even out in the summer months and only slightly differ toward the later part of the season. Mean annual relative humidity for the entire study is 70% (National Oceanic and Atmospheric Administration 1983).

METHODS

The prairies were surveyed between May 1983 and March 1984 for presence/absence data for each bryophyte species in each prairie. Each prairie was visited twice during this period. Collecting was concentrated in the open prairie (for this paper open prairie is defined as that area dominated by typical prairie grasses and forbs), but some collections were made in small stands of trees within the prairie. All collections were made by the author and are deposited in the Institute for Botanical Exploration (IBE) herbarium, Mississippi State University, and the author's personal herbarium. Nomenclature follows Crum and Anderson (1981) for the musci and Stolter and Crandall-Stolter (1977) for the Hepaticae.

A Sorenson's Index of Similarity (IS_s = c/.5 [A + B]) was used to express how related the study sites were in quantitative representation of bryophyte taxa.

RESULTS AND DISCUSSION

A total of 28 species of mosses and 2 species of liverworts were collected from 12 prairies in western Missouri and western Arkansas (Table 1). The study resulted in 9 new county records for Missouri and 5 for Arkansas. *Weissia controversa* Hedw., *Atrichum angustatum* (Brid.) BSG, *Campylium hispidulum* Mitt., and *Amblystegium varium* (Hedw.) Lindb. were collected from at least 7 of the 12 prairies. These species were commonly encountered throughout the prairies in which they were found. *Weissia controversa* Hedw. was found on all the prairies, while *Campylium hispidulum* Mitt. and *Amblystegium varium* (Hedw.) Lindb. were collected from all except Dorsett Hill for the former and Stump prairie for the latter.

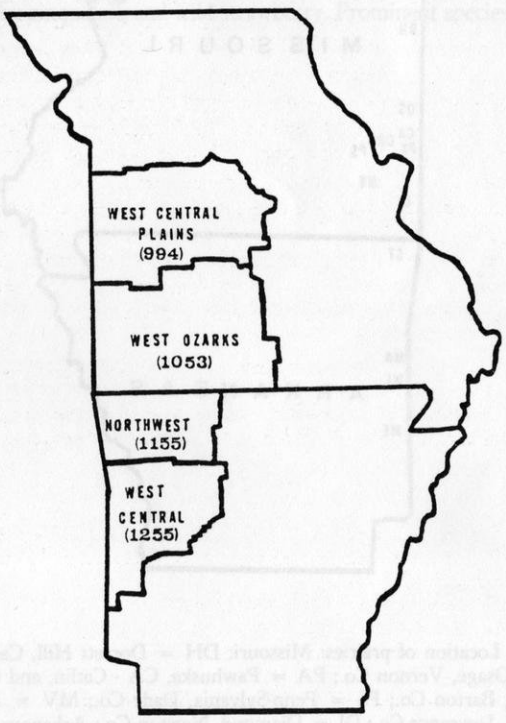

FIG. 2. Climatic divisions with mean annual precipitation (in millimeters).

Weissia controversa Hedw. is considered to be a common weedy species of disturbed sites (Crum and Anderson 1981). Its success on prairies may be attributed to the management techniques employed. Arkansas prairies are mowed and/or hayed yearly while the preserved prairies of Missouri are under a strict management program which alternates haying and burning. Numerous studies have found these techniques to enhance the growth of the vascular vegetation on prairies of Missouri and Arkansas (Kucera and Ehrenreich 1962, Dale 1983). It seems probable that these management practices would also play an important role in the establishment and reproductive success of prairie bryophytes, but this has yet to be reported. Prairie management would result in an increase in light intensity and temperature reaching the soil surface. The more successful species would be those adapted to tolerate this increase in light intensity and temperature. Other species may become established once sufficient growth of the vascular vegetation occurred. *Weissia controversa* Hedw. may be a successful prairie species due to its photosynthetic capabilities at high light intensities and temperatures. O'Keefe van der Linden and Farrar (1983) report that this attains its highest rate of photosythesis at 40° C. Hosokawa and Odani (1957) suggest that certain species of bryophytes are adapted to, and require, high levels of light for maximum photosynthesis.

Campylium hispidulum Mitt. was found on all prairies with the exception of Dorsett Hill. This species is considered by the author to be a commonly encountered prairie species of southwest Missouri and western Arkansas. Timme (1983) found it to be the most common species encountered on a prairie in southwest Missouri. Crum and Anderson (1981) report the species to be found in rather moist forest of eastern North America while Reese (1984) reported it to be found in dry to mesic forest in the Gulf South.

Amblystegium varium (Hedw.) Lindb. was not found on Stump prairie in northwest Arkansas but was found on all the other prairies studied. This species occupies various habitats, often being found in rather dry places (Crum and Anderson 1981). It was frequently collected throughout the prairies studied.

The remaining taxa were only sporadically collected and therefore considered minor community components of the prairies studies at this time.

The Sorensen Index of Similarity (Sørensen 1948) was used to compare the bryological similarity of the 12 prairies (Table 2). Churchill (1982) considered a 50% or higher similarity index to indicate a relatively high degree of similarity. Results of the present study indicate all the prairies to have indices of 50% or higher, except Dorsett Hill and Catlin. This indicates that most of the prairies are similar bryologically throughout the study area.

Dorsett Hill had indices less than 50% for all prairies except Massard, Pawhuska, and Stump. The indices for these prairies are 55, 60, and 55 respectively. These values are among the lowest when compared to all other indices. Dorsett Hill is a 195 ha prairie knoll approximately 100 feet higher than the surrounding area and is completely enclosed by an upland hardwood forest. According to Toney (1978) this feature adds to the prairie's rich vascular species composition. At this time it is not known why Dorsett Hill differs bryofloristically from the other prairies. It may be due to topography or the surrounding vegetation, or it may simply be that further detailed collecting is needed.

Catlin prairie is also a prairie completely enclosed by a hardwood forest. However, the trees on its eastern boundary form only a narrow band (× 15 m). This prairie has similarity indices below 50% for 3 of the total surveyed. As before, the causes of these differences are not known.

TABLE 1. Prairies from which each taxon was collected. Abbreviations for prairies are the same as in Fig. 1.

	CA	DH	DI	GO	MA	ME	MV	OS	PA	PS	ST	WV
Amblystegium varium	x	x	x	x	x	x	x	x	x	x		x
Atrichum angustatum			x		x	x		x	x	x	x	
Aulacomnium palustre						x						
Brachythecium oxycladon					x							x
B. rutabulum		x										
Bryoandersonia illecebra						x						
Bryum caespiticium								x				
B. capillare		x										
B. pseudotriquetrum	x											x
Campylium chrysophyllum	x									x	x	
C. hispidulum	x		x	x	x	x	x	x	x	x	x	x
Clasmatodon parvulus											x	
Dicranella heteromalla			x					x				
Ditrichum pallidum	x	x			x	x			x		x	
Entodon seductrix	x	x			x					x		
Ephemerum crassinervium				x								
Eurhynchium hians				x								
Fissidens bushii	x											
F. taxifolius	x											
Fosstroemia trichomitria										x		
Frullania inflata					x						x	
Lejeunea glaucescens					x							
Leskea gracilescens		x	x	x	x							x
L. obscura									x			
Leucodon julaceous	x											
Mnium cuspidatum		x							x			
Orthotrichum pusillum					x							
Rhynchostegium serrulatum		x										
Thuidium delicatulum					x							
Weissia controversa	x	x	x	x	x	x	x	x	x	x	x	x

TABLE 2. Sorensen Similarity Index of mosses collected from western Missouri and western Arkansas prairies. Numbers presented are for taxa collected from open prairie only. IS = c/0.5 (A + B) x 100 where IS = Sorensen's Index of Similarity, c = number of species held in common by two prairies, A = total number of taxa in first prairie, B = total number of taxa in second prairie. Underlined numbers are the total taxa from each prairie. Numbers in parentheses are the number of taxa held in common in the two prairies. Abbreviations for prairies are the same as in Fig. 1.

	CA	DH	DI	GO	MA	ME	MV	OS	PA	PS	ST	WV
CA	8	46	50	50	62	53	54	46	62	62	71	46
DH	(3)	5	44	44	55	46	40	40	60	40	55	40
DI	(3)	(3)	4	75	80	54	86	89	89	89	80	67
GO	(3)	(2)	(3)	4	60	55	67	86	67	67	60	67
MA	(4)	(3)	(3)	(3)	6	62	67	73	90	73	83	73
ME	(4)	(3)	(3)	(3)	(4)	7	60	50	67	50	61	50
MV	(3)	(2)	(3)	(3)	(3)	(3)	3	75	75	75	67	75
OS	(3)	(2)	(4)	(3)	(4)	(3)	(3)	5	80	80	72	60
PA	(4)	(3)	(3)	(3)	(5)	(4)	(3)	(4)	5	80	90	60
PS	(4)	(2)	(4)	(3)	(4)	(3)	(3)	(4)	(4)	5	90	60
ST	(4)	(3)	(4)	(3)	(5)	(4)	(3)	(4)	(5)	(5)	6	55
WV	(3)	(2)	(3)	(3)	(4)	(3)	(3)	(3)	(3)	(3)	(3)	5

Current bryological studies of tallgrass prairies in Missouri and Arkansas have resulted in further understanding of species distribution. These studies have raised questions about what factors cause some prairies in western Missouri and western Arkansas to differ bryofloristically, if indeed they do, and what factors are involved in the success of bryophytes on these prairies. Future studies will entertain these questions and continue to investigate the distribution of prairie bryophytes. It is hoped that these studies will eventually develop a bryogeographical overview of the tall grass prairies of the midwestern United States.

The following annotated list of taxa is alphabetical by family (family name is given in parentheses with the first genus of the family). Habitat for all taxa is open prairie unless otherwise noted. Taxa preceded by an asterisk are new county records (county and collection number are listed following the taxon).

Hepaticae

Frullania inflata Gott. (Jubulaceae). On bark of *Ulmus americana*.
Lejeunea glaucescens Gott. (Lejeuneaceae). On bark of *Ulmus americana*.

Musci

**Amblystegium varium* (Hedw.) Lindb. (Amblystegiaceae) Vernon and Barton Co., MO. 3803 and 3754 respectively; Sabastian and Polk Co., AR. 4092a and 4076 respectively.
Campylium chrysophyllum (Brid.) J. Lange.
Campylium hispidulum Mitt.
**Aulacomnium palustre* (Hedw.) Schwaegr. (Aulacomniaceae). Polk Co., AR. 4073.
**Brachythecium oxycladon* (Brid.) Jaeg. and Sauerb. (Brachytheciaceae). Sebastian Co., AR. 3784.
**Brachythecium rutabulum* (Hedw.) BSG. Cass Co., MO. 3820.
Bryoandersonia illecebra (Hedw.) Robins.

**Eurhynium hians* (Hedw.) Sande-Lac. Polk Co., AR. 4077.
Rhynchostegium serrulatum (Hedw.) Jaeg. and Sauerb. On soil of prairie/forest border.
Bryum caespiticium Hedw. (Bryaceae). **Bryum capillare* Hedw. Cass Co., MO. 3815.
Bryum pseudotriquetrum (Hedw.) Gaertn., Meyer and Scherb.
**Fosstroemia trichomitria* (Hedw.) Lindb. (Cryphaeaceae). On bark of *Ulmus americana*. Barton Co., MO. 3761.
Dicranella heteromalla (Hedw.) Schimp. (Dicranaceae).
**Ditrichum pallidum* (Hedw.) Hampe. (Ditrichaceae). Cass Co., MO. 3814b.
Entodon seductrix (Hedw.) C. Muell. (Entodontaceae). On bark at base of *Quercus*.
**Ephemerum crassinervium* (Schwaegr.) Hampe. (Ephemeraceae). Barton Co., MO. 3746.
Clasmatodon parvulus (Hampe) Hook. and Wils. *ex* Sull. (Fabroniaceae). On bark of *Juniperus virginiana*.
**Fissidens bushii* (Card. and Ther.) Card. and Ther. (Fissidentaceae). Barton Co., MO. 3794.
Fissidens taxifolius Hedw.
Leskea gracilescens Hedw. (Leskeaceae). On bark at base of *Ulmus americana*.
Leskea obsura Hedw. On bark at base of *Ulmus americana*.
Leucodon julaceus (Hedw.) Sull. (Leucodontaceae). On bark of *Ulmus americana*.
Mnium cuspidatum Hedw. (Mniaceae). On soil at prairie/forest border.
Orthotrichum pusillum Mitt. (Orthotrichaceae). On bark of *Quercus*.
Atrichum angustatum (Brid.) BSG. (Polytrichaceae).
**Weissia controversa* Hedw. (Pottiaceae). Cass Co., MO. 3817.
Thuidium delicatulum (Hedw.) BSG. (Thuidiaceae). On soil near stream.

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VEGETATION DYNAMICS IN THE DELTA MARSH, MANITOBA

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Abstract. Freshwater marshes are dynamic ecosystems characterized by cycles of flooding and drying. The 15,000 ha Delta Marsh at the south end of Lake Manitoba was formed about 2,500 years ago. Several channels permit an exchange of water between the lake and the marsh so that their water levels have fluctuated in unison. Traditionally, the marsh has undergone cycles of flooding and drying with four such cycles from 1914-1960. The last natural flood peaked in 1955, killing 20% of the emergent vegetation. Recolonization began in 1958 as water levels fell. Prominent pioneer species included *Scolochloa festucacea, Chenopodium rubrum, Ranunculus sceleratus, Aster laurentianus, Atriplex patula, Rumex maritimus* var. *fueginus* and *Senecio congestus*. Within three years, parts of most marsh shores, sloughs and ponds were again dominated by the emergents *Phragmites australis, Typha* spp. and *Scirpus* spp. while *Scolochloa festucacea, Carex atherodes* and *Calamagrostis canadensis* formed the wet meadow vegetation. In 1961, a regulation regime was imposed upon Lake Manitoba that reduced water level fluctuations from 2.1 to 0.6 m, virtually eliminating traditional flooding and drying cycles. Since 1961, emergent vegetation has expanded rapidly throughout the marsh. Several schemes for rehabilitating the marsh have been proposed, but none have yet been adopted. It is essential to restore some form of the natural water cycle if the marsh is to survive.

INTRODUCTION

Prairie marshes depend upon cycles of flooding and drying for their survival (e.g., van der Valk and Davis 1978). Periodic floods of several years duration kill emergent vegetation while drying phases promote the germination of buried seeds and the establishment of new stands of emergents. This paper describes the effects of a flooding-drying cycle (from 1953-1961) on the emergent vegetation of Delta Marsh, and vegetation changes following the 1961 construction of a water control structure that stabilized water levels in Lake Manitoba and the marsh.

The Delta Marsh is the largest freshwater marsh in the Canadian prairies. It covers 15,000 ha, extending 28 km from east to west and up to 6 km from the shores of Lake Manitoba in the north, to the agricultural Portage Plain in the south (Fig. 1). The marsh consists of a chain of shallow bays connected by narrow channels and separated from the south end of the lake by a barrier ridge. The bays range in size from a few to several hundred hectares and average about 1 m in depth with a maximum of 3 m. Linear sloughs which represent former drainage channels extend into the

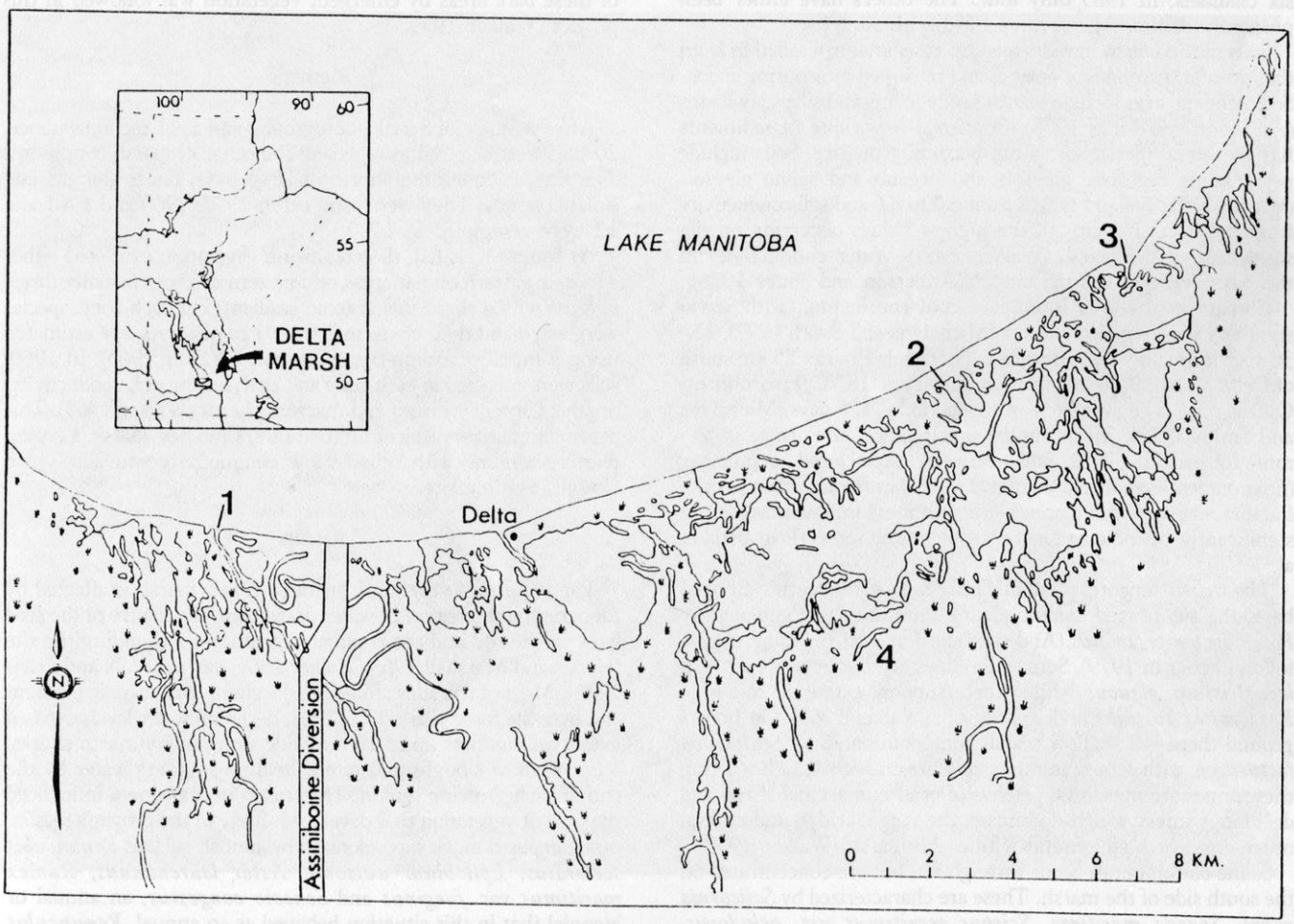

FIG. 1. Delta Marsh in southern Manitoba. 1: Cram Creek, 2: Chimney Marsh, 3: Clandeboye Channel, 4: Tin Town Slough.

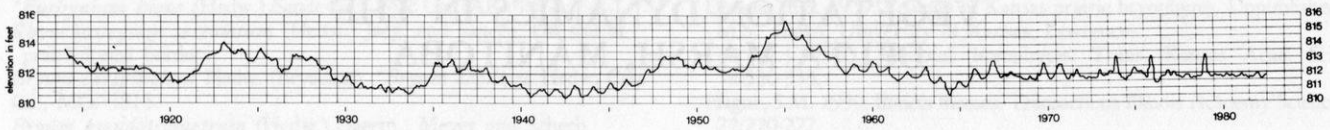

FIG. 2. Water level fluctuations in Lake Manitoba, 1914-1982. Courtesy Water Resources, Province of Manitoba.

plain to the south. Small shallow ponds occur throughout.

Beginning about 4,500 years ago, a sandy delta was constructed in the southwestern part of Lake Manitoba at the mouth of a distributary channel of the ancestral Assiniboine River (Teller and Last 1981). Subsequently, the river ceased to flow into Lake Manitoba and instead flowed eastward. By 2,500 years ago, some of the deltaic sands had become reworked to form a barrier beach along the south end of the lake, thereby isolating an extensive marsh. Since its creation, the marsh has undergone several major vegetation cycles, probably reflecting several major episodes of high and low water. These cycles are inferred from fluctuations in pollen and seed assemblages in cores taken in one of the bays of the marsh (Sproule 1972).

Throughout its history, Delta Marsh has been connected to Lake Manitoba by several channels through the barrier ridge and these have allowed water to pass between the marsh and the lake. Thus, episodes of high and low water in the lake have produced cycles of flooding and drying in the marsh, but over the years, the number of channels has been reduced. In 1925 there were six channels; in 1985 only four. The others have either been purposely dammed or become filled with silt.

Soils in the marsh have formed from sediments washed in from the lake and surrounding uplands and reworked by scouring action. Sediment textures include loams, sandy loams and silty clay loams (Anderson and Jones 1976). Continual reworking of sediments has prevented marsh soils from becoming mature. Soils include peaty saline regosolic gleysols and organo and saline gleysols (Walker 1965). Soil pH ranges from 6.0 to 8.6 and soil conductivity from 0.2 to 54 mS cm^{-1}, the highest values occurring on the south side of the marsh (Walker 1965). Water conductivity in the bays averages 3.2 mS cm^{-1} (Anderson and Jones 1976).

Climate in the area is mild to cool continental, with warm summers and long cold winters (Michalyna and Smith 1972). The 30-year mean July temperature at Portage la Prairie, 25 km south of Delta Marsh, is 20° C; that for January is -18° C (Environment Canada n.d.). The average frost-free period is 128 days (Michalyna and Smith 1972). Mean annual precipitation at Portage is 545 mm, of which 70% falls between April and September (Environment Canada n.d.). Annual rainfall in the Canadian prairies fluctuates in a cyclical manner although these fluctuations are not significantly periodic to form a regular time series (Pospahala et al. 1974).

The marsh supports predominantly freshwater species. In open bays, the submerged aquatic plant community is dominated by *Potamogeton pectinatus* (Anderson and Jones 1976: Nomenclature follows Scoggan 1979). Some shorelines are bordered by *Scirpus lacustris* ssp. *glaucus* while others support extensive stands of *Phragmites australis* and *Typha* spp. (Walker 1965). On higher ground there is a shallow marsh zone dominated by *Scolochloa festucacea* with lesser amounts of *Carex atherodes*. Bordering these zones are meadows, patches of prairie, marginal shrub and deciduous forest which dominates the barrier ridge and several other areas of high ground within the marsh (Walker 1959).

Saline communities occur throughout, but are concentrated on the south side of the marsh. These are characterized by *Salicornia rubra, Suaeda maritima, Scirpus maritimus* var. *paludosus, Puccinellia nuttalliana, Triglochin maritima* and *Hordeum jubatum*.

VEGETATION CHANGES DURING A FLOODING-DRYING CYCLE, 1953-1961

There were four major cycles of high and low water in Lake Manitoba between 1914 and 1960 (Fig. 2). The most recent high water episode began in 1953 with lake levels reaching a peak in 1955 at 1.05 m above the 40-year mean of 251 m (815.87 ft.). During several storms in the summer of 1955, strong northwesterly winds forced water over and through the ridge into the marsh. These wind set-ups aggravated the flood situation in the marsh. Water levels began to drop in 1956, and fell to the 40-year mean by late 1958. Minor fluctuations characterized the next two years.

These high waters from 1953-58 flooded approximately 20% of the emergent vegetation (Dillon 1956), killing hundreds of hectares of *Phragmites australis, Typha latifolia* and *Scirpus* spp. By 1958, the marsh consisted of expanses of open water surrounded by tracts of stubble and bare organic muck. Almost all the herbaceous vegetation was killed except a few stands of *Phragmites australis* in the higher margins of the marsh. The colonization of these bare areas by emergent vegetation was followed in this project (Walker 1959, 1965).

Methods

After a study of aerial photographs and field reconnaissance, 20 sites were selected to represent the range of marsh conditions. The sites included the shores of large bays, linear sloughs and isolated ponds. They were sampled in 1959, 1960 and 1961 and 12 were resampled in 1980.

As water levels fell, the colonizing vegetation exhibited either a mosaic pattern on flat areas or a pattern of zones (usually three) in areas with a slight topographic gradient. For each zone, species were listed and their cover in 20, 1 x 1 m quadrats was estimated using a modified Braun-Blanquet scale (Walker 1965). In 1960, soils were collected in each zone and analyzed for pH, conductivity, organic content, texture and macronutrients (Walker 1965). This paper summarizes results from two sites: Chimney Marsh, a typical marsh shoreline with soils of low conductivity and Tin Town Slough, a saline site.

Results

The pattern of vegetation succession in a marsh is affected by topography, the season of water drawdown, the nature of the seed bank in the soil and the residual vegetation surrounding the site (Harris and Marshall 1963, Walker 1965, van der Valk and Davis 1978). Most of the sites studied had a slight topographic gradient and over the three years, 1959-1961, declining water levels exposed extensive mudflats up to 100 m wide along many marsh shores. Some shallow sloughs and ponds held no standing water by the end of each growing season. The season of drawdown influenced the type of vegetation that developed. Early in the growing season, newly exposed muck was colonized by annuals such as *Ranunculus sceleratus, Epilobium watsonii, Aster laurentianus, Rumex maritimus* var. *fueginus* and *Senecio congestus*, an annual or biennial that in this situation behaved as an annual. *Ranunculus* and *Senecio* are short-lived; they generally flower, set seed and die before the end of July. Later in the season they may be replaced

by other annuals such as *Chenopodium rubrum, Atriplex patula* and the seedlings of perennials such as *Scolochloa festucacea* and *Typha* spp.

Although no comprehensive studies of marsh seed banks were carried out during the 1953-1961 cycle, recent analyses of bottom muck from open bays and experimental impoundments in the marsh indicated that some of the pioneers and dominant emergents were well represented in the seed bank (Pederson 1981): *Typha* spp., *Scirpus lacustris* ssp. *validus, Chenopodium rubrum, Ranunculus sceleratus, Carex atherodes, Scolochloa festucacea* and *Atriplex patula*. Those poorly represented in the seed bank included *Scirpus maritimus* var. *paludosus, S. lacustris* ssp. *glaucus* and *Phragmites australis*, all perennials with vigorous vegetative reproduction. Throughout the three-year study, for example, *Phragmites australis* expanded rapidly from residual stands by means of underground rhizomes and runners that extended along the ground surface (Walker 1965). Seeds of other species (e.g., *Sonchus* spp.) probably blew into the area of developing vegetation after drawdown.

Chimney Marsh. This marsh shore, 10.9 km east of the Delta channel, is typical of sites along the south side of the forested ridge (Fig. 1). Organic content and soil texture varied widely within the site; conductivity averaged 0.3 mS cm^{-1} and pH 7.2 (n = 5). As water levels declined, vast areas of *Phragmites australis* stubble were exposed and a zoned pattern of vegetation developed (Figs. 3 and 4).

In late June 1959, the area nearest the retreating water (Zone 1) was dominated by seedlings of *Scolochloa festucacea* (Table 1) associated with *Ranunculus sceleratus* and *Epilobium watsonii, Lemna minor* covered many of the shallow depressions. The slightly higher ground of Zone 2 had been exposed the previous year. In it *Scolochloa* and *Calamagrostis canadensis* grew up to 1 m tall and had an understory of *Mentha arvensis, Galium trifidum, Scutellaria epilobiifolia*, seedlings of *Typha* spp., and 12 species of minor importance (Walker 1965).

Because many pioneer species are short-lived, the composition of the zones had changed by August 1959. Zone 1 was still dominated by *Scolochloa* but frequent *Cicuta maculata* and *Typha* spp. had replaced *R. sceleratus* and *E. watsonii*. Zone 2 contained *Calamagrostis, Carex atherodes* and *Scolochloa* understoried by *Mentha arvensis* and *Sonchus arvensis* (Table 1). A higher, third zone contained *Eupatorium purpureum* var. *maculatum* and *Calamagrostis canadensis*.

By August 1960, an additional 15 m of shallow water and exposed organic muck had been colonized. Zone 1 was a mosaic of *Phragmites* stubble and water. The water was covered with *Lemna minor* while the low mounds of stubble were colonized by *Chenopodium rubrum, Ranunculus sceleratus* and seedlings of *Typha* spp., *Sonchus arvensis* var. *glabrescens* and *Cicuta maculata*. In Zone 2, *Scolochloa festucacea* grew in organic muck with *Typha* spp., *Sonchus arvensis* and *Mentha arvensis*. Zone 3 contained 12 species. *Calamagrostis canadensis* was dominant with an understory of *Mentha arvensis* and *Urtica dioica*. A fourth zone with *Eupatorium purpureum, Solidago canadensis, Carex atherodes* and *Cirsium arvense* was evident on the highest parts of the site adjacent to the forested barrier ridge (Walker 1965).

In 1961, the newly-exposed muck of Zone 1 was again colonized

FIG. 3. Aerial view of Chimney Marsh in 1959, showing (right to left) Lake Manitoba, the forested barrier ridge, marginal *Salix* shrub, emergent vegetation in a zoned pattern, and denuded areas of shallow water with *Phragmites australis* stubble.

by *Chenopodium rubrum*. It was associated with *Aster laurentianus, Typha* spp. seedlings, *Ranunculus sceleratus* and *Senecio congestus*. Zone 2 was waterlogged and dominated by *Scolochloa festucacea, Carex atherodes* and *Typha* spp. Zone 3 was now a better-drained transition between the marsh and the forested ridge. It was dominated by *Calamagrostis canadensis* with frequent *Epilobium watsonii* and *Urtica dioica*.

Tin Town Slough. The most easterly of the shallow temporary drainage channels or sloughs is approximately 3.8 km long and 30-40 m wide. It lies 0.5 km south of the shores of a large bay (Fig. 1). Soil texture and organic content varied as at Chimney Marsh. Mean soil pH was 7.1 (n = 8) and mean conductivity was 7.9 mS cm^{-1} (n = 8) (Walker 1965).

Water was present in the slough early in the 1959 season but none remained when sampling occurred in early September. Zone 1, the low-lying center of the channel, contained *Chenopodium rubrum* and occasional *Hordeum jubatum* and *Aster laurentianus* (Table 2). Zone 2 was colonized by *Scolochloa festucacea* with a few scattered plants of *Spartina pectinata*. Zone 3, dominated by *Spartina pectinata* with an understory of *Hordeum jubatum*, was distinct from a fourth zone of *Hordeum jubatum* and *Atriplex patula* with scattered clumps of *Phragmites australis* that had survived the flood.

In June 1960, approximately 30 cm of water covered the dead shoots of the previous year's *Scolochloa festucacea*. By September, the center of the slough (Zone 1) had dried up, and was dominated by *Chenopodium rubrum* with patches of *Scirpus maritimus* var. *paludosus* and *Hordeum jubatum*. Zone 2 continued to be dominated by *Scolochloa festucacea* with *Hordeum jubatum* and *Atriplex patula*. *Phragmites australis* had spread vegetatively into Zone 3 from higher ground and was understoried by *Sonchus arvensis* and *Atriplex patula*.

In 1961, *Scolochloa festucacea* and *Hordeum jubatum* covered the center of the slough (Zone 1) and *Rumex maritimus* var. *fueginus* was occasional. A border of *Scolochloa* formed the second zone, its low growth contrasting with the marginal zone of tall *Phragmites* (Zone 3) with an understory of *Sonchus arvensis* and *Atriplex patula*.

VEGETATION CHANGES UNDER STABLE WATER LEVELS, 1961-1980

Efforts by the Provincial government to regulate water levels in Lake Manitoba began as early as 1904 (Manitoba Water Comm. 1973). It was not until 1961, however, when a control structure was built at the lake's outlet, that these efforts succeeded. Since 1961 (Fig. 2), lake levels have been held within a 0.6 m range compared with the unregulated range of 2.1 m (Bodnaruk 1976). Delta Marsh water level fluctuations have thus been reduced, virtually eliminating the traditional marsh water cycle of flooding and drying. Other construction works have inhibited the free exchange of water between the lake and the marsh. Completed in 1969, the Assiniboine Diversion carries spring floodwater from the Assiniboine River at Portage la Prairie to Lake Manitoba. The channel, which cuts through the marsh (Fig. 1), effectively prevents the interchange of water from Cram Creek to parts of the west marsh.

Stable water levels in the marsh over the past two decades have permitted the spread of emergent communities. All of the 20 sites surveyed in 1959-61 supported dense stands of emergent vegetation by 1980 or earlier.

When Chimney Marsh was revisited in 1980, the vegetation fringing the *Salix* spp. thicket along the southern margin of the forested ridge was dominated by *Calamagrostis canadensis* with frequent *Eupatorium purpureum, Cirsium arvense* and occasional *Carex atherodes* (Fig. 4). Immediately south was an almost pure stand of *C. atherodes* with scattered patches of *Scolochloa festucacea*. Beyond this, a zone of *Phragmites australis* several

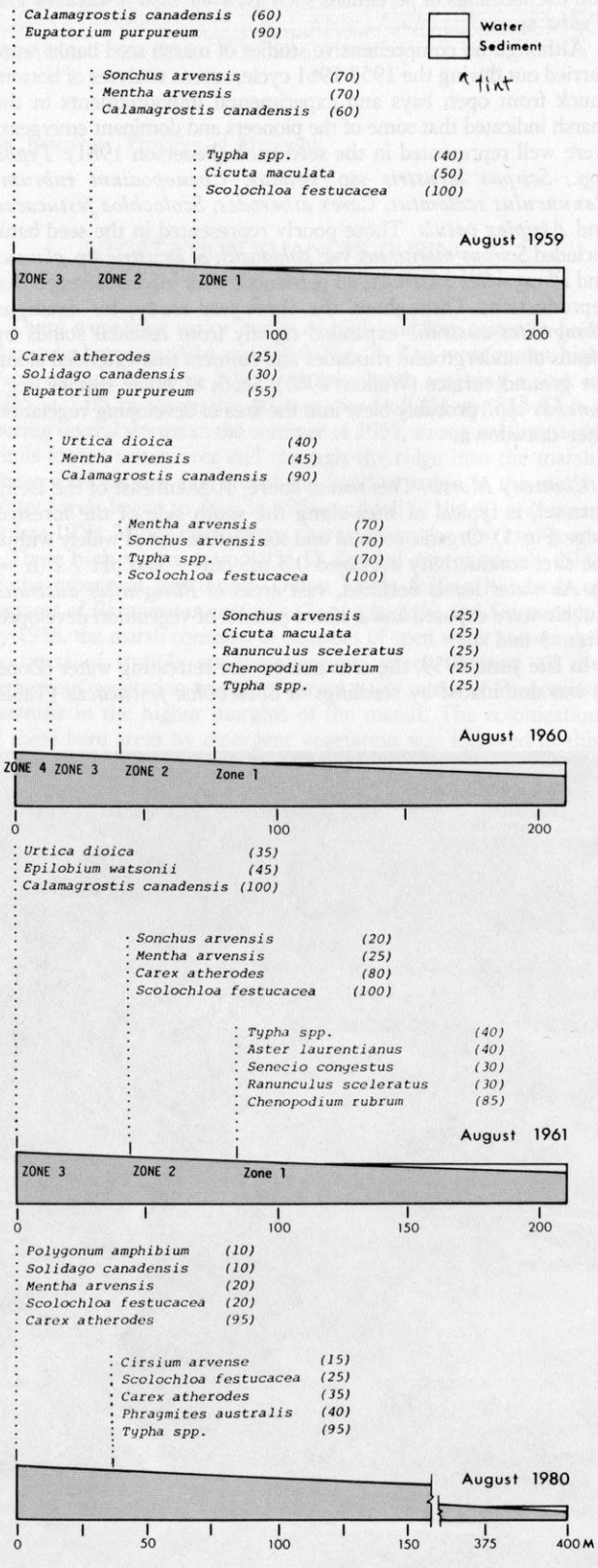

FIG. 4. Profiles across Chimney Marsh in 1959, 1960, 1961 and 1980 showing vegetation zones. Species with frequencies < 10% are omitted. Frequency percentages are in parentheses.

TABLE 1. Selected species from Chimney Marsh, 1959 - 1961.

	Wet----------										----------Dry
	Frequency %										
	Zone 1				Zone 2				Zone 3		
Species	1959[1]	1959[2]	1960[3]	1961[4]	1959[1]*	1959[2]	1960[3]	1961[4]	1959[1]	1960[2]	1961[3]
Scolochloa festucacea	80	100	-	-	74	30	100	100	20	15	20
Ranunculus sceleratus	65	-	25	30	5	-	-	-	-	-	-
Epilobium watsonii	40	10	-	5	10	-	-	-	-	-	45
Lemna minor	30	-	25	5	25	-	-	-	5	-	-
Carex atherodes	15	-	-	-	32	40	55	80	-	5	10
Chenopodium rubrum	10	-	25	85	-	-	-	-	-	-	-
Galium trifidum	10	20	-	-	47	-	-	10	-	-	-
Mentha arvensis	10	20	-	-	90	70	70	25	-	45	20
Senecio congestus	10	-	-	30	-	-	-	-	-	-	-
Sonchus arvensis	10	-	25	10	26	70	70	20	40	15	25
Cicuta maculata	5	20	25	-	22	10	-	-	-	-	-
Typha spp.	5	40	25	40	37	20	70	75	20	10	15
Aster laurentianus	-	-	-	45	26	-	-	-	-	5	-
Phragmites australis	-	-	-	10	16	-	-	-	-	-	15
Eupatorium purpureum	-	-	-	-	10	-	-	-	90	35	-
Scutellaria epilobiifolia	-	-	-	-	42	-	-	-	-	-	5
Calamagrostis canadensis	-	-	-	-	47	60	5	10	60	90	100
Urtica dioica	-	-	-	-	26	10	-	-	20	40	35
Cirsium arvense	-	-	-	-	16	-	-	-	-	15	20

Sampling dates (1) 29 June 1959
(2) 17 August 1959
(3) 4 August 1960
(4) 3 July 1961

* n = 19

TABLE 2. Selected species from Tin Town Slough, 1959 - 1961.

	Wet----------									----------Dry
	Frequency %									
	Zone 1			Zone 2			Zone 3			
Species	1959[1]	1960[2]	1961[3]	1959[1]	1960[2]*	1961[3]	1959[1]	1960[2]	1961[3]	
Chenopodium rubrum	95	80	-	-	22	-	-	-	-	
Scirpus maritimus	20	75	-	-	-	-	-	-	-	
Hordeum jubatum	30	35	65	-	44	15	45	-	75	
Rumex maritimus	20	-	30	-	-	-	-	-	-	
Aster laurentianus	30	-	-	-	-	-	-	-	-	
Scolochloa festucacea	5	20	75	100	100	100	10	-	75	
Spartina pectinata	-	-	-	10	5	-	100	-	-	
Phragmites australis	-	-	5	-	5	-	10	65	100	
Sonchus arvensis	-	-	15	-	-	15	-	50	100	
Atriplex patula	-	-	-	-	38	-	-	50	100	

Sampling dates - (1) 6 September, 1959
(2) 14 September, 1960
(3) 5 July, 1961

* n = 18

meters wide gave way to a dense expanse of *Typha* spp. (*T. glauca*, with some *T. latifolia* and *T. angustifolia*) that extended for approximately 300 m to open water. Slightly higher areas within the *Typha* stand bore a mixture of *C. atherodes* and *Scolochloa festucacea* with occasional *Mentha arvensis* and *Scutellaria galericulata*. In slight depressions with water up to 25 cm deep, *Utricularia vulgaris* and *Lemna minor* flourished.

Tin Town Slough in 1980 showed two zones of vegetation. The lower central part of the drainage channel was dominated by *Carex atherodes* with occasional *Scolochloa festucacea* and a few shoots of *Phragmites australis*. Both margins of the slough bore dense monodominant stands of *Phragmites australis*.

This expansion of emergent vegetation has resulted in a marked reduction in the number of small ponds and sloughs. Many have been colonized by dense stands of *Typha* spp. which presently thrives in places where periodic flooding by wind set-up occurs. On slightly higher ground *Phragmites australis* grows in dense stands. An example of in-filling has been documented for Crescent Pond near Cram Creek, using aerial photographs taken over the past several decades (Goldsborough 1984). There was a decrease of 25% in the area of open water in the pond from 1964-1980. At this rate, the pond will be completely overgrown by emergent vegetation by the year 2027.

CONCLUDING COMMENTS

In order to remain viable and to contain a diversity of habitats, freshwater marshes must undergo periodic cycles of flooding and drying. Ideally, the flooding phase should be long enough to kill emergent vegetation and the drying phase long enough to permit the emergents to recolonize the denuded areas. Delta Marsh has traditionally experienced such cycles of flooding and drying. Its water levels are linked with those of Lake Manitoba, which from 1914-1960 experienced four cycles of high and low water.

In 1961, however, cycles in the marsh were virtually eliminated by a control structure that has permitted Lake Manitoba water levels to be artificially stabilized. The Assiniboine River diversion has further complicated the marsh water cycle by reducing the interchange of water between the lake and parts of the west marsh. One consequence of these modifications is that there has been no elimination of emergent vegetation by flooding since the high waters of the mid-1950's. Indeed, there has been a marked expansion of emergent vegetation throughout the marsh.

What of the future? For nearly two decades various government and private agencies have advanced proposals aimed at some form of restoration of the traditional water cycle. One option that has not been widely discussed is to allow Lake Manitoba to occasionally fluctuate within its traditional range and thus restore a flooding and drying cycle to the marsh. The timing could be predetermined. Such a program would necessitate control over, or compensation for the lands that would be periodically flooded. It would not involve costly construction works or complicated management plans, but would restore a regime similar to that which sustained the Delta Marsh and other marshes in the Lake Manitoba basin for the last two millennia.

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Part 3. DESCRIPTION AND CLASSIFICATION OF GRASSLAND VEGETATION

DESCRIPTION OF COMPLEXITY IN PRAIRIES THROUGH HIERARCHY THEORY

T.F.H. ALLEN and T.W. HOEKSTRA

Abstract. Classifications of prairies are classifications of descriptions of prairies not of the prairies themselves. Descriptions are scale dependent and so it is important that the entities classified are equivalently scaled. Failure to achieve equivalent scaling will create artifactual differences leading to confusion of natural classes. Adjustments to the scale of entities can be made by changing the extent of the data set or by transforming the data to some more or less coarse grained form (e.g., from quantitative to qualitative form). However, recognition of the achievement of the appropriate scale should be by some consistent ecological phenomenon exhibited by the modified data (e.g., fire seen as external to the system as opposed to an internal process).

INTRODUCTION

The description and classification of prairies is such a challenge that a whole conference session has been devoted to it. One way to meet the problem is to invest effort in description of particular prairies and develop methods and classification schemes that are consistent with the data. There is, however, something to be said for a more general approach, one that attempts to define the fundamental nature of the problem of prairie description.

At the heart of the problem is the essential complexity of prairie vegetation. That would seem to be a reasonable point of departure since the complexity of the vegetation in these biomes is something upon which ecologists can agree. However, having agreed on the question of prairie complexity, it is not transparent what that consensus means. Without a definition of complexity, all we have achieved is a tacit agreement not to question the fact that we do not and cannot understand how the individual plants, populations and species in aggregate amount to the whole prairie.

Complexity arises when adequate description requires more than one level to be considered at once (Allen and Starr 1982). An explanation always involves offering relationships at some lower level as an account of behavior at the upper level. The situation becomes more complex the more fine grained are the things whose relationship constitutes the explanation. The fineness of grain here is a relative matter, relative that is to the size of the thing requiring explanation. The larger is the thing at the upper level, the more detail that is being considered. When the distinctions at the lowest level are very fine, it is only possible to link the upper level to its explanation by using intermediate levels where distinctions are made less finely. It is in this way that many levels of organization enter into a complex explanation.

Prairies are complex because ecologists see them as containing a lot of plants belonging to a large number of species, most of which seem relevant to an adequate account of vegetation structure and function. The intermediate levels that help link the prairie system to its plants are levels where the separate plants are aggregated into coarser units such as guilds. Prairie is undeniably complex but this is a comment about the requirements for adequate explanation. It is always easier to conceive of tangibles like organisms than intangibles like guilds. The appeal of these tangibles as the proper level of explanation is great.

Even a small amount of homogeneous gas can be seen as complex if one insists on looking at individual atoms within. Nevertheless, such a gas can for many conditions be dismissed as simple, for example, in its adherence to Boyle's Law. The complexity that we acknowledge for prairies comes from an insistence on recognizing the plant types as different and their interactions as various. The fact that prairies can be readily seen as complex does not belong to the prairies independent of observation and explanation, any more than the homogeneous gas is intrinsically simple because Boyle's Law is a fair approximation for a small part of its behavior. This is not to deny that prairies are seen to consist of many different species to a good taxonomist. The complexity comes from the decision to reduce prairies all the way to the level of those species and even to organisms and their interactions. Complexity comes from the fineness of distinctions that are made at the level which is accepted as adequate for explanation. That prairies can be reduced to organisms and species is a property of the prairies themselves, but the complexity comes from our choice of that level for explanation.

DISCUSSION

Hierarchy Theory

There is body of theory that considers exactly these problems and it is called hierarchy theory. Levels of organization are central to hierarchy theory although, according to Allen and Starr (1982), there need be no assertion that the levels are real beyond a device for observation.

Given levels are defined by observable entities that show certain characteristic return times in their cycles of behavior. For example, a given prairie burns at regular intervals of about 2.5 years in length, but a prairie considered as soil builder has its level defined by the long time periods associated with that process. The prairie seen as a soil builder requires the fire cycle as one of its internal processes; the slow soil building level is explained in part by the lower fire cycle level with its rapid nutrient cycling behavior. Levels are defined by the cycling times of their recurrent behavior, and the levels are ordered relative to one another by the relative lengths of those time periods. Since larger things generally behave more slowly than small things, upper levels generally involve physically larger structures. For example the burning prairie vegetation with its short periodicities for recurrence is a subset of the slow behaving vegetation-soil complex. The vegetation is physically smaller than its landscape.

Note that the above uses only observational criteria to define the relationships. The role of the observer is well defined in hierarchy theory and indeed that is one of the advantages of the approach (Allen et al. 1984). Observation is predicated upon a subjective choice, the recognition of entities which are the objects of study. These entities are defined by a certain set of criteria, but as with all definitions, the defining criteria are arbitrary.

Whether or not the world presents us with configurations that meet the definitions (i.e., whether we find the entities we seek) is not arbitrary but the criteria used for recognition are inevitably of the observer's choosing. This fastidious separation of the observer from the observed gives a certain flexibility and frees the ecologist from the burden of meaningless decisions as to whether or not his classes are real in an ontological sense. We do not need to know whether or not our classification of prairies is fundamentally correct, we need only seek classifications which are useful. Of course it is essential that the observations be correctly classified in the chosen frame, but that is a different question. The take home message is: let the observations guide the formulation of the classification scheme rather than assert that this or that scheme is correct.

As the observer makes his decisions as to what entities he will observe, he determines to an extent what will be the level of discourse. The level is completely fixed when he also decides how often he will observe and for how long. It is not possible to observe levels that involve periodicities shorter than the time between samples; nor is it possible to focus upon entities that have a period of characteristic behavior longer than the entire sampling period. It is the time and space characteristics of the observational protocol that determine the level that will be observed.

Incorporation of Disturbance

Before dealing with problems in Prairie Classification it is useful to consider scale and the incorporation of disturbance. The discussion has thus far has been of observables and observation. Note that most observations are of stable entities or relationships because the observed world is held in those configurations more of the time; stability is, therefore, involved in the discussion at least implicitly. Stability is central to an understanding of the relationship between levels.

One of the concerns of hierarchy theory is the generation of higher levels of organization from lower levels. The emergence of new levels very much involves stability or, rather, instability. The pioneering research in this field was performed by Prigogine (1978) working on nonequilibrium thermodynamics in chemical systems. Unlikely as it may seem, discoveries there apply broadly and even to prairies.

Higher levels can be profitably seen as constraints applied to contain instabilities at the lower levels. When one considers fire in prairies, two levels are readily distinguishable. At the lower level fire is seen as a signal (perturbation in the mathematical sense) coming from outside the system; every time there is a fire it changes the prairie - we all know the beautiful show of fall composites that is the response of the prairie to a spring burn. The higher level addresses a larger entity and is more inclusive. At the higher level, the prairie includes fire as a working part of the system; fire at this level does not deliver a signal that changes the prairie, for regular fire is required to keep the prairie in a constant state of health.

In the example above, the two levels can be seen in an evolutionary context such that the lower level is what is left of the primitive system now set in the context of adaptation to fire. Vegetation faced with fire is at first disturbed. However, when the fire returns it addresses a vegetation modified by fire. Only those that can survive the fire or return quickly after it are there to be burned again. Repeat this process several times and the result is a fire adapted community. The individual fires do have an effect but they are now set in a context that incorporates them into the system such that fire no longer disturbs. In fact in a fire adapted community, withholding fire would be the disturbance. In prairie vegetation fire has been incorporated into the system.

Scaling Problems in Prairie Classsification

It is possible to use the rather esoteric considerations of thermodynamics of nonequilibrium chemical systems to address the very practical matters of how best to observe and classify prairies. Since there are several perfectly valid levels from which to choose, it emerges that there is no one best way to observe and describe prairies, but only ways to observe and arrange the data at different levels of organization. Furthermore descriptions at different levels are contradictory. In the example above, fire is not only a disturbance at the lower level but also a stabilizer at the higher level, both at the same time. This is a clear contradiction but one that is accommodated by a change in level. The contradictions that emerge with description at different levels are clearly a wide open invitation to confused classification.

The major difficulty in classification is to describe all the items to be classified at a consistent level of organization. Problems arise from the fact that it is very easy to change the level of description by slight adjustments in procedures of data collection, transformation or analysis. Allen and Wiley to (1983) were able to describe the Curtis Prairie at two levels by making moderate adjustments in the analysis of a single data set. They performed ordination on some data of permanent quadrats. Their approach employed transformation of cover data to presence lists as a tool to cut into the prairie at different levels of organization.

Cover data make fine grain distinctions between the performances of plants and allow analysis to focus upon which plants do well under which circumstances. Presence data are more coarse grained in the distinctions they make. In suppressing information about which plants are growing vigorously, presence data emphasize species tolerances. For a plant to show patterns of cover variations, it must be present in the first place. Presence data, with their coarse grained distinctions, therefore describe the slow behaving context in which the cover data show their patterns of behavior. The presence data pertain to a higher level of organization.

After ordination of the permanent quadrats, two forms of fire data were superimposed on the ordination diagrams. If quadrats that had been recently burned clustered together, this would be taken to mean that individual fires were responsible for the patterns in the vegetation data. If quadrats that had been burned the same number of times in the last five years all clustered together, this would be taken to mean that not individual fires, but rather the burning regime was responsible for the patterns in the vegetation data. If individual fires order the data, then fire can be seen as an influence coming from outside the vegetation pattern. If individual fires do not order the data but patterns of burning over the years do, then individual fires can be considered as part of the system maintaining a healthy prairie. Analysis of cover data showed fire as a disturbance while presence/absence data showed it as a stabilizing force. In general, the more coarse grained are the distinctions in the data after transformation, the higher will be the level of organization that emerges from the analysis. Furthermore the more heterogeneous the data set, the higher will be the emerging level. The same is true the larger is the data set: bigger ecological structures emerge (Allen and Starr 1982).

Despite these helpful rules of thumb, it is not usually at all clear which level is likely to emerge from a given analysis. This is because size and heterogeneity of the data set and the coarseness of grain of the data transformation may counteract each other. Unfortunately we do not have the experience, at the moment, in using this new way of viewing data analysis to know what to expect. For example, does a coarse grained transformation applied to a large homogeneous data set give the same level of description as a fine grained transformation applied to a small heterogeneous data set? At this point we do not exactly know the answer. Nevertheless, we would expect them to be of the same order, because the heterogeneity of the second set will be counterbalanced by the smallness of the first set and the fine grain of its data transformation, but we cannot be sure. Worse than this, the

heterogeneity of the data set is commonly an unknown because, despite our best efforts to control data collection procedures for consistency, the degree of natural variation in the vegetation is not controlled and may not be read accurately.

Even so there is a way out of the problem and it is one that has already been found by the good intuition of the skilled investigators of prairies. What we offer here is a formal statement and derivation of what is common sense and good practice. Upper levels are more inclusive than lower levels and that is why the level of description that sees fire as a stabilizing part of the system is higher than the level of description that sees fire as outside the system and a perturbation. The level of description is recognizable from what is seen to be inside the system and what is seen to be outside. It is crucial that the ecologist identify his level of description not from his procedures of data collection and analysis, but from the patterns of behavior of a particularly scaled ecological phenomenon in his results. Let the ecology give the label rather than leaving it to some poorly understood mathematical procedure.

No matter what the data transformation or heterogeneity of the data set, if individual fires change prairie structure as seen in the analysis, then the level of description is fine grained enough so that fire is outside the system. If that is the level of description desired then all is well, but if the description at hand is of a higher level where fire is an integral part of the system, then changing the grain of the data transformation or the size of the data set may allow the pattern of fire as a disturbance to emerge. If the pattern which does emerge shows fire as a disturbance, then the analyst is not only describing the system at the level he chooses, but he knows that to be the case. The important thing for prairie classification is that the level of description of the prairies compared by classification should be the same for all the prairies in the classification. The ecologist can be assured of this if and only if the scale is determined by some specific and explicit criterion.

The scaling criterion we have used is fire, but we hasten to add that it is only an example. It is a particularly good one for our purposes because of the obvious conflict between the levels of description where fire is a disturbance on the one hand, but also a stabilizer on the other. Comparison between prairies described at different levels would be just as problematic even if fire were not mentioned, but the error might be more insidious because the conflict between the differently scaled descriptions might not be so obvious. The criteria that are available for standardizing the scale are numerous.

Dix (1959) in his study of Wisconsin dry lime prairies used grazing pressure as his ordering criterion. He achieved consistent scaling by carefully considering his prairies in pairs, one grazed and one ungrazed, commonly on opposite sides of a fence and never more than a quarter of a mile apart. By focusing on just that one criterion, he was able to compare validly prairies from all across southern Wisconsin. Some of his findings were at odds with prairie patterns ordered by some other criteria. He found some counter-intuitive responses of some species along his grazing gradient only because his gradient was ordered by such a specific criterion. Grazing was the criterion that he used to scale his analysis; the scale chosen for observation and description was one where grazing was seen as a perturbation from outside the system. This does not deny that buffalo grazing is part of the prairie landscape, it is just that such an account uses a different and higher level for description. Note also that Dix's work involved a different type of herbivore in a different grazing situation.

CONCLUSION

We have shown that comparison, namely classification, of prairies is fraught with danger. The difficulty upon which we have focused is that of scaling. Comparison between prairies using differently scaled descriptions is not valid. The difficulty is one of finding which scale is being used in each description so that a standard can be imposed. If a prairie were described at two different levels, a classification including those two descriptions would probably separate them as belonging to different classes of prairie. This would happen even though it was the selfsame patch of vegetation that was described, let alone descriptions of two different prairies that should belong in the same class. Differences in the scale of descriptions break up natural classes of vegetation.

The procedure that we recommend for avoiding scaling problems is the imposition of some very specific scaling criteria. Any attempt at a broad general purpose classification of prairies is doomed to failure because it will only be by chance that the entities being classified are equivalently scaled. Classifications are specific to particular purposes and become at best confused, and at worst misleading, if there are no specific ecological purposes state at the outset.

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DEVELOPMENT OF A VEGETATION-BASED APPROACH TO SITE CLASSIFICATION

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Abstract. This paper traces the historical development of using vegetation to develop a natural classification system for wildland sites. Emphasis is placed on ecological concepts, classification concepts, methodology and applications to management. The aim of the paper is to remove some of the mystique and clarify some of the apparent confusion surrounding the realm of ecological land classification.

INTRODUCTION

This symposium provides a timely forum to discuss ideas and methods regarding the intricate relationships between vegetation classification and site classification. Although my personal experience deals primarily with forest communities, we share a common heritage in plant ecology.

The purpose of my paper is to briefly review:

1. Development of the habitat type classification system based on vegetation.
2. Development of the range site system (from an observer's perspective).
3. A general comparison of range sites and habitat types.

I considered rehashing debates on: taxonomy vs. mapping, science vs. dogma, plant ecologists vs. soil scientists, foresters vs. range managers, scientists vs. managers, continuum vs. discreteness, and uniformity vs. creativity. However, my aim is not to fuel the debates that often rage over these issues, but rather to encourage common understanding. Since the amount of debate on an issue is often inversely proportional to the amount of knowledge, let us seek to find our common agreement and then seek to find out where we have areas of disagreement. These can become the focus for gaining new knowledge.

Numerous symposia have been held on definition and classification of ecosystems. One notable example was entitled, "Can we find a common ground in forest ecosystem classification" (IX International Botanical Congress in Montreal in 1959) - published in *Silvae Fennica* in 1960. The problems, viewpoints and conclusions are just as pertinent for prairie ecosystems.

Rather than attempt to provide a complete literature review, let me trace the development of one system currently being developed on a wide scale throughout the western United States (for details see Pfister 1984).

FOREST HABITAT TYPE CLASSIFICATION

1890-1950 - Concepts

Plant associations were first described in the European literature in the late 1800's. Concepts of using climax plant communities as a basis for forest site classification were expounded in the early 1900's (e.g., Korstian 1917, 1919). During the first half of the century many ideas were explored and debated, but little progress was made on development of a vegetative-site classification system with direct application to forest management.

1952 - Association and Habitat Type Taxonomy

Daubenmire's (1952) forest associations for northern Idaho represent the first operational taxonomy (key provided) and the first actual use of the term "habitat type." The choice of term is appropriate when one relates it to the definition of the term "association." Please note that Daubenmire used association in the narrow sense - restricted to climax vegetation types. Furthermore, these associations represent only primary climaxes as defined by Tansley (1935). Disclimaxes are treated as "secondary" derivations maintained by the influences of an external factor.

1960's - Cautious Use and Expansion

During this period some specialists began to relate the habitat type taxonomy to timber productivity, silviculture, soils, range and wildlife. Simultaneously, several of Daubenmire's graduate students began to develop similar taxonomic classifications for surrounding areas.

1970's - Rapid Expansion and Application

Major programs were established to expand coverage of the classification system to new areas. Sampling and analysis techniques were improved to provide more rapid coverage (e.g., Pfister and Arno 1980). In areas where the taxonomy was completed, work was initiated on mapping, developing management implications for the types, and utilizing the system in planning.

Concepts of land and resource classification were reviewed to resolve questions of alternative classification approaches and interrelationships (Bailey et al. 1978). Work on a proposed interagency national land (site) classification system progressed throughout the decade.

1980's - Widespread Use, Expansion and Reflection

Use of the forest associations (and habitat types) has spread widely through the general forestry profession. Work is underway to complete geographic coverage. Studies are continuing to determine and document management implications and relationships to the types. Causal factors continue to be explored and several scientists are working on determining successional relationships within the environmental strata defined by the habitat types. The Series and Association (*sensu* climax) are incorporated in the proposed component land classification system for the United States (Driscoll et al. 1983).

RANGE SITE CLASSIFICATION

For a forest ecologist to attempt to trace the development of the range site concept may sound unrealistic. But, let me share the perspective I have gained from the literature without the benefit of application experience.

Concepts

Shiflet (1975) suggested that an early publication by Korstian (1919) may have provided the basic concept and thinking for range sites. In reading this article, I was impressed by Korstian's foresight and the quality of his arguments for development of a site classification system - regarding sites as "integral biological units," reflecting the "combined effect of the climatic and edaphic conditions of the forest stands should be based on the potentiality

of the site.'' Shiflet (1975) suggested that this concept was transposed from forest lands to rangelands during the 1930's and 1940's. Although Korstian's statements have stood the test of time, I suspect that the range site concept evolved from an ecological background independently and in a parallel fashion to the habitat type concept rather than being ''transposed'' from forestlands to rangelands. Dyksterhuis (1958) stated that ''synecology became the foundation for a range evaluation procedure'' and did not even cite Korstian!

Range Condition

The concept of range condition was established by Sampson (1917) with range condition classes defined as departures of the present vegetation from the original (or climax) vegetation of the site. This represented application of the Clementsian concept of plant succession and climax to practical range problems. Problems in application of the concept and quantification of condition classes were prevalent because the range sites were not adequately defined. ''Since range condition expresses departure from potential for a site, it followed that delineation of sites had to precede delineation of range condition classes'' (Dyksterhuis 1949).

Range Site - 1940's

This concept evidently emerged during the late 1940's as a response to the practical need to establish a benchmark for quantitative derivation of condition classes. Range sites were delineated on the basis of differences in relative coverage in the climax (Dyksterhuis 1949). Workers were making the transition from the monoclimax concepts of Clements to the more practical polyclimax concept of Tansley with ''climax referring to climatic, edaphic or physiographic climaxes.'' Site separation is considered justified if: (1) there is a measurable difference in species composition of the climax or (2) there is sufficient difference in productivity to justify recommending a different rate of stocking'' (Dyksterhuis 1949). The program was developed as an operational system for field technicians, including (evidently) the delineation and quantitative description of the climax vegetation types (range sites) by the field technicians for their own areas of study.

Range Site - 1950 to Present

Dyksterhuis (1958) presented a noble defense of an operational system developed for practical range management application. However, it also revealed annoyance with the ''academic types'' who were not reluctant to criticize an approach that appeared to be dogmatically provincial within the range profession. Although the statement is made that, ''despite necessary approximations, the natural and stable (vegetation) types provide the logical basis for any classification of range sites,'' a transition had been made to naming the range sites on the basis of physical features. Renner and Allred (1962) documented these ideas in a USDA Agricultural Handbook which evidently has become the standard for the Soil Conservation Service, the Bureau of Land Management and many range management professionals.

Grassland Habitat Types

During this same period other research on natural grasslands resulted in a formal classification of habitat types (Daubenmire 1970). Presumably this contribution would have provided the quantitative descriptions needed for practical, operational range evaluation procedures. Yet, Daubenmire did not provide any discussion on relationships with range site. Furthermore, his analysis of the poor relationship between associations and either climatic variables or soil types presumably raised concerns among range site proponents. A later publication by Mueggler and Stewart (1978) provided additional impetus to the recognition of habitat types as an alternative to the range site approach. Numerous recent studies are also developing habitat type taxonomies, several of which are reported on in this symposium.

The Current Range Site-Habitat Type Debate

Prior to this symposium two points of view were expressed which indicated that range management professionals were concerned about the evolution of rangeland habitat types. Anderson (1983) defended his personal definition of an ''ecological site'' as a broader concept than ''range site'' and stated that an ''ecological site'' has inherent management implications whereas a ''habitat type'' does not. He further distinguished ''habitat type'' as an academic tool and ''ecological site'' as a management tool and urged professors to strengthen this distinction for their students' benefit. Dyksterhuis (1983) made a similar attack on habitat types, obviously as a defense of the established operational procedures of the range site system.

Since the time of this symposium, Hoffman (1984) and Daubenmire (1984) have responded by strongly emphasizing the positive aspects of the habitat type concept and applications to practical forest and rangeland management. It appears that the range management profession is approaching a crossroads where understanding both approaches is crucial as different agencies and individuals are pursuing different paths toward the same objective.

DISCUSSION

Forest habitat type classifications evolved from the discipline of plant ecology. Continued development is also carried out primarily by plant ecologists or foresters with an advanced degree in plant ecology. Their purpose is to provide a standard syntaxonomy, a description of the potential stable vegetation types (climax association), description of the physical environment and a key to the habitat types (land areas). Foresters and technicians are then trained to identify the types, consider management implications and map habitat types for planning purposes. The taxonomy provides the long-term foundation to expand management implication criteria for mapping and a framework to evaluate successional relationships.

Range site classifications have also evolved from the discipline of plant ecology. The original concept of using potential climax vegetation as the foundation is very similar. But this is where the similarity ends. By 1949, production had been included as a secondary basis to delineate range sites. During the 1950's, the process of defining range sites evolved features. Also, the methodology used in developing a taxonomy of range sites contrasts strongly with that used in the habitat type approach.

As rangeland habitat type classifications become available for new areas where range sites are being used, operational and conceptual concerns naturally begin to surface. Proponents often try to support their own position by strong criticism of the alternative approach, rather than looking at objective comparisons. Each system has some strong points and some weak points.

When habitat type classifications first become available the management implications are only partially developed. Familiarity with the system must be gained before other people begin to develop and summarize the management knowledge pertaining to each type. Identification of disturbed sites may be difficult and extrapolation based on similar local soils and topographic situations may be necessary.

Numerous examples can be cited of the dangers of extrapolating site factor-habitat type correlations beyond the area for which the relationships were developed. This is to be expected because of two basic ecological principles: (1) vegetation serves as an integrator of the total physical environment, and (2) compensating factors allow similar vegetation to develop on sites with strongly contrasting individual site factors. Thus, the correlation of individual site factors with habitat types is often less than suspected and desired by many.

When range sites are defined and mapped according to physical site factors, the perceived or real lack of correspondence to potential vegetation types will continually prevent scientific acceptance of the operational approach. Range scientists and students need to face this problem by interacting and exchanging ideas with plant ecologists, rather than retreating to a range management dogma. Although range site and habitat type were originally similar in concept, the operational procedures for range site identification have evolved much closer to a direct physical factor approach.

I suggest that the major problem common to either approach is the unspecified and usually unknown correlation of specific individual physical site factors with the climax vegetation types. In the habitat type approach, this problem does not surface until the user is faced with mapping or identifying disturbed areas. In the range site approach, this problem is inherent in the methodology of defining range sites on the basis of physical features and defining the vegetation parameters characteristic of the range site without knowing the variation or specific degree of correlation.

Each of you must come to your own conclusions regarding these questions. The literature cited will lead you to many more references which you may find interesting or frustrating depending on your objective or point of view. One method of resolution may be to conduct objective field comparisons of alternative classifications on the same piece of ground.

CHALLENGES

The ecosystem concept provides a strong foundation for looking at interrelationships and interactions from a holistic viewpoint. But, it is also a two-edged sword because none of us can describe and interpret all of these interactions. Simplication and isolation of factors is necessary for interpretations. We must work with approximations and modify these as we learn more. Ecologists should be humble in their ignorance and continually seek new insights. I will take the liberty to offer you some challenges:

To Scientists and Educators

1. Provide a foundation of the state-of-knowledge that is clearly enunciated and concisely documented as the building blocks for new knowledge.
2. Continually challenge dogma and suggest fruitful areas of research - to point out what we know and readily admit what we do not know.

To Students

1. Diligently seek to understand the concepts, principles and arguments - their basis and perspective.
2. Evaluate arguments on the basis of alternative viewpoints from various perspectives rather than right vs. wrong.
3. Beware of premature condemnation of alternative perspectives.

To Land Managers

1. Tolerate criticism of "what is" based on a theoretical viewpoint of "what could be."
2. Utilize new knowledge to improve management objectives.
3. Be open-minded and objective in considering new knowledge and techniques.
4. Function as professionals - utilize the latitude provided within your agency. In the long run the agency operatives reflect the professionalism of the employees at all levels of management.

A SPECIFIC CHALLENGE FOR PRAIRIE VEGETATION CLASSIFICATION

Utilize the current high level of scientific activity to coordinate and cooperate in the establishment of some pilot demonstration areas for training and education. For the same areas define and map range sites and independently do the same for habitat types. Compare the maps and the types. Test the correlation of key site factors with vegetation. Prepare a joint publication on the results with a co-author from each background. I will look forward to future programs of the North American Prairie Conference in the hope of seeing such an article.

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THE CONCEPT OF HABITAT TYPES IN THE CLASSIFICATION OF LANDS SUPPORTING GRASSLAND VEGETATION

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Abstract. A habitat type is that land area which supports, or is capable of supporting, the same climax vegetation. The concept is applicable to grasslands in both basic and applied contexts. The concept provides a means of classifying grasslands which is consistent with the same concept used in classifying National Forest lands over much of the Rocky Mountains.

INTRODUCTION

The aim of this paper is to discuss the concept of habitat types (HT's) with special reference to lands supporting grassland, and rangeland vegetation.

The HT concept was defined by Daubenmire (1952). Later the Daubenmires (1968) described in detail the forest HT's of eastern Washington and adjacent Idaho, and in 1970 Daubenmire described the grassland HT's of eastern Washington. The 1968 and 1970 monographs are the first complete descriptions of forest and grassland HT's for a given geographic region. In numerous later studies investigators have adopted the same ecologic concept in describing HT's for various other regions, mostly in the western United States. The U.S. Forest Service has sponsored most of these studies; their aim has been to have described all the major HT's in the Rocky Mountain Region. This has been an impressive endeavor and the results will represent a classification of forested lands of the largest geographic area over which the sampling scheme and the ecologic interpretation of the vegetation has been uniform throughout. The stand data, published by the U.S. Forest Service primarily, are relatively complete records of the vegetation and in some cases of soil data, physiographic data, animal components, pests, etc. The records are valuable for later verification, refinement, or modification by other investigators. Where remnants of climax vegetation are being eliminated, the stand data recorded may be the only record remaining which adds to its importance.

A significant beginning has also been made to describe grassland HT's over parts of western United States (Francis 1983, Francis and Aldon 1983, Hansen, Hoffman and Bjugstad 1984, Hansen and Hoffman 1985, Hironaka, Fosberg and Winward 1983, Jorgensen 1979, McLean 1970, Mueggler and Stewart 1980, Tisdale 1979).

DEFINITIONS

Because of apparent confusion and misunderstanding among some range scientists regarding HT's (Dyksterhuis 1983, Anderson 1983) it is appropriate to present here definitions of certain terms used in the concept of HT's. One assumes, initially, that the classification of vegetation, and/or the lands supporting it is a worthy endeavor. Certainly much time and effort has been devoted to it by those in both basic and applied areas of ecology. Management of grasslands and/or forest lands is certainly enhanced by a classification of some kind.

Climax vegetation — that which has attained an equilibrium with its environment such that species population structures no longer exhibit unidirectional change.

Climatic climax vegetation — that which occurs on normal topography, over deep, loamy, moderately well-drained soils.

Edaphic climax vegetation — that which is distinct from climatic climax vegetation as a result of stable soil characteristics which differ from those of soils supporting climatic climax vegetation.

Topographic climax vegetation — that which is distinct from climatic climax vegetation as a result of the predominant influence of topography which fosters a microclimate with distinctive vegetation.

Fire climax — stable vegetation which is distinguished by the influence of periodic recurring fires.

Zootic climax — stable vegetation which is distinguished by the influence of a particular level and intensity of animal influence.

Fire climax and zootic climax are **disclimaxes** (disturbance climaxes), and climatic, edaphic, and topographic climaxes are **primary climaxes**. If the recurring disturbance of fire or grazing were removed, the disclimax would theoretically change in a direction of developing into one of the primary climaxes. Only primary climaxes are the bases of determining habitst types.

Habitat type — those land areas which support, or are capable of supporting, a distinctive climax vegetation.

APPLICATION OF THE HABITAT TYPE CONCEPT

The words above and the concept of succession are not new in the ecological literature, and the concept of HT's is not a radical idea. Assuming the definitions given above, which are based to a considerable extent on Tansley's 1935 paper, are sound theoretically and can be demonstrated in the field, then the HT concept should provide a rational ecological basis of land classification. If site potential is best indicated by the vegetation, as generally thought, then climax, or near-climax vegetation probably is the best indicator of site potential (Alexander 1974, Major 1978). Recognizing site potential in terms of such vegetation requires an understanding of both vegetation dynamics and the autecologies of the species involved. Once completed, a study to delimit HT's of a region should yield a valuable framework on which to base additional studies and plans for management as well.

The HT concept can apply to range management, which is an applied science. Some apparent confusion among range scientists regarding the HT concept (Dyksterhuis 1983, Anderson 1983) stems from less than an ecologic view of their resource - range or rangeland both terms of which are rather ill-defined and arbitrary in a landscape classification. In Oregon Anderson (1983) observed the *Agropyron spicatum* - *Festuca idahoensis* HT on north-facing slopes at 1,000′ elevation under 9-12″ ppt., on undulating topography at 2,000′ elevation under 12-15″ ppt., and on south-facing slopes above 4,000′ elevation under 15-20″ ppt. That environmental factors compensate for one another along environmental gradients has been an axiom of ecology for many years and the presence of the *Agropyron* - *Festuca* HT on north-facing slopes at low elevations, on uplands at intermediate elevations, and on south-facing slopes at high elevations illustrates the principle. The essentially identical stands of this HT possibly represent the site potential to best advantage, and if this is true, then "ecological site" (*sensu* Anderson 1983) must refer to something other than climax or near climax stands of vegetation (Daubenmire 1984, Hoffman 1984). If the fundamental difference between HT and "ecological site" concepts is that management strategies can be inferred only from "ecological site," this can be true only by definition. We seem to be hung up with definitions. By definition 90% of the rangeland in South Dakota can be classified into 10 range sites, modified to a degree by geographic location in the state (Schumacher and Johnson 1980). The authors point out that

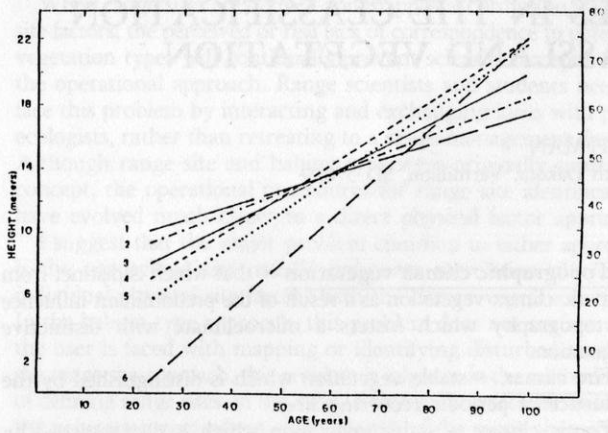

FIG. 1. Linear regressions of height on age of *Pinus ponderosa* in these habitat types of the Black Hills National Forest: 1. *Pinus ponderosa* - *Symphoricarpos albus*; 2. *Pinus ponderosa* - *Juniperus communis*; 3. *Pinus ponderosa* - *Arctostaphylos uva-ursi*; 4. *Picea glauca* - *Vaccinium scoparium*; 5. *Pinus ponderosa* - *Carex foenea*; 6. *Pinus ponderosa* - *Oryzopsis asperifolia*. Redrawn from Rioux (1984).

the full name of each range site includes the soil name and geographic area and this identifies the "natural plant potential." Even though the names of the range sites do not include plant names, the designations "Silty Western" or "Clayey Eastern" must relate that which is pertinent about "natural plant potential" for these two range sites in South Dakota. In the Black Hills of South Dakota and Wyoming the *Pinus ponderosa* - *Juniperus communis* HT occurs at elevations of 5,000′ to 7,150′ on level to sloping topography with slopes up to 17%, and on aspects ranging from 0° to 350°. Additionally, soil textures range from clay loam to silt loam, loam, and to sandy loam. We have also shown that a relationship exists between growth of ponderosa pine and HT in the Black Hills (Fig. 1). If sites of the HT's described for the Black Hills were classified using a range site grouping, many would be regrouped differently than HT's would indicate. Though sites of the *Pinus* - *Juniperus* HT indicate similarities in potential vegetation, they apparently are of different ecological sites (*sensu* Anderson 1983) and of different range sites (Schumacher and Johnson 1980). Whether or not a range site classification would ever be attempted in the Black Hills is irrelevant. What is relevant is whether or not a basic ecological concept is applicable to forests, grasslands, shrublands, etc. It seems apparent that land classification concepts expressed by Schumacher and Johnson (1980) and by Anderson (1983) are specialized for very limited use, and have little ecological basis.

In western North Dakota, South Dakota and adjacent Montana we have described HT's of both grassland and forest (Hansen et al. 1984, Hansen and Hoffman 1985). In this region the following are HT's which support climatic climax vegetation:

Stipa comata - *Carex filifolia* HT
Stipa comata - *Carex heliophila* HT
Festuca idahoensis - *Carex heliophila* HT

In this region the complex topographic and edaphic conditions have resulted in a complex vegetational pattern. In all we described 21 HT's of which 18 are edaphic or topographic climaxes. The *Agropyron smithii* - *Carex filifolia* HT is one of the edaphic climaxes. Under grazing, stands of the *Stipa comata* - *Carex filifolia* and *Agropyron smithii* - *Carex filifolia* HT's gain a considerable degree of similarity. This results from a decline in vigor and abundance of both *Stipa* and *Agropyron* and an increase in the vigor and abundance of *Bouteloua gracilis* which is common to both HT's. Vegetation of these two HT's may then be lumped into a single vegetation type dominated by *Bouteloua gracilis*. Whether these two HT's should be distinguished by the range managers can only be answered by them. The plant ecologist would separate them on the basis of perhaps only a few plant species plus some consistent environmental distinctions. Certain it is that range site designations such as "silty," "clayey," or "sandy" (Schumacher and Johnson 1980) will not distinguish these two HT's, nor most others we have studied in this region.

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SELECTED HABITAT TYPES OF THE CUSTER NATIONAL FOREST

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Abstract. We have identified and delimited 21 habitat types in the Grand River/Cedar River, Sioux, and Ashland Districts of the Custer National Forest. These include 4 woodland and forest habitat types. The vegetation was sampled using the methods of Daubenmire and Daubenmire (1968) and Daubenmire (1970). We sampled stands that were nearly mature, judged to be most homogeneous, and least disturbed by fire, trails, past farming, or grazing. The steppe and forest habitat types described are the *Stipa comata/Carex filifolia, Stipa comata/Carex heliophila, Festuca idahoensis/Carex heliophila*, and *Fraxinus pennsylvanica/Prunus virginiana* habitat types.

INTRODUCTION

The Grand River/Cedar River, Sioux and Ashland Districts of the Custer National Forest occur in northwestern South Dakota, southwestern North Dakota, and southeastern Montana. The region supports steppe, woodland, and forest vegetation. The aim of the present paper is to briefly describe the major steppe and forest vegetation of this region, their distributions and changes resulting from domestic animal grazing.

THE STUDY REGION

The study region is part of the Missouri Plateau of the Great Plains Province (Fenneman 1931). It is characterized by broad areas of grassland on Cretaceous and Tertiary substrates. Alluvial valleys, many of which still support gallery forests, mark the drainageways through the region. The region also features tablelands some of which are capped with resistant sandstone.

The study region includes the Grand River/Cedar River, Sioux and Ashland Districts of the Custer National Forest. The Grand River/Cedar River District includes the Grand River National Grassland in South Dakota and the Cedar River National Grassland in North Dakota.

The Grand River/Cedar River District is a moderately dissected upland plain with a few prominent buttes and ridges. The main drainages are the Grand River and Cedar River which flow eastward to the Missouri River. The Sioux District is located in southeastern Montana and northwestern South Dakota. Prominent in this district are sandstone buttes and hills, rising to 100-300 m above the surrounding landscape. All are geologic remnants of the Tertiary Fort Union Formation overlying Cretaceous tablelands (Stone et al. 1983). The main drainages are the Grand, Moreau, and Little Missouri Rivers which flow north- and eastward to the Missouri River. The Ashland District lies between the Tongue River and the Powder River in southeastern Montana. The surface consists of the Tongue River member of the Fort Union Formation (Warren 1959). Where large areas of lignite beds have burned, heat has baked and oxidized adjacent shales producing a brittle, reddish iron-oxide colored porcelainite, locally called scoria and clinker beds. Common landscape features include badlands, sandstones, shale escarpments, and scoria buttes with highly irregular topography. The main drainages are the Tongue River and the Powder River which flow northward to the Yellowstone River.

The climate of the region is relatively xeric. Annual precipitation of a few locations across the region from west to east are as follows (U.S. Dept. of Commerce 1960a, 1960b, 1960c):

Billings, MT	332.7 mm	Beach, ND	377.4 mm
Miles City, MT	324.5 mm	Dickinson, ND	393.5 mm
Ekalaka, MT	337.1 mm	Bismarck, ND	391.2 mm
Sheridan, WY	402.1 mm		

There is a slight increase in annual precipitation eastward across the region. The higher value for Sheridan, Wyoming reflects the influence of the Bighorn Mountains on southeasterly winds in the area.

METHODS

We followed methods developed by Daubenmire and Daubenmire (1968) and Daubenmire (1970). First we traveled over the entire region to become familiar with possible habitat types, and to collect plants. We noted locations of all areas least disturbed by grazing, the locations of exclosures, and the occurrence of possible sites for intensive study. Based on reconnaissance of the first summer, and continuing reconnaissance during the second and third summers, we sampled 150 sites. At each grassland site we estimated canopy coverage for each species within 50 - 2 x 5 dm plots placed at 1 m intervals along a 50 m tape.

In forests and woodlands we set up 15 x 25 m plots. On hillsides these were placed with the long direction along the contour of the slope. Each plot was subdivided into three 5 x 25 m subplots. Trees were counted and recorded by dm dbh size classes throughout the plot. Undergrowth coverage estimates were made within 50 - 2 x 5 dm microplots placed at 1 m intervals along the inner sides of a central 5 x 25 m subplot. We chose for sampling the most homogeneous part of each stand (Daubenmire 1970). We determined homogeneity subjectively. We avoided obvious discontinuities and sharp breaks in the microtopography of any stand, and locally disturbed areas, such as animal trails. The tentative list of habitat types developed in 1981 was both substantiated and altered as the result of our sampling and additional reconnaissance in 1982 and 1983.

MAJOR STEPPE VEGETATION

Stipa comata/Carex filifolia Habitat Type

The *Stipa comata/Carex filifolia* habitat type is widespread in the Grand River/Cedar River District and the eastern half of the Sioux District. It occurs on nearly level plateaus, isolated buttes, and gentle slopes that appear to be relatively free from excessive erosion. *Stipa comata* and *Carex filifolia* dominate the vegetation. *Agropyron smithii, Bouteloua gracilis, Artemisia frigida* and *Koeleria pyramidata* provide limited additional coverage (Table 1). *Agropyron cristatum* once was planted over much of the region,

TABLE 1. Constancy and mean coverage of shrubs, graminoids and forbs that attain a constancy of 75% or more in the *Stipa comata/Carex filifolia* habitat type. Values are based on data of 18 stands.

Species	Constancy	Mean Coverage
Stipa comata	100%	76.8%
Carex filifolia	100	53.1
Bouteloua gracilis	100	6.5
Agropyron smithii	94	10.4
Artemisia frigida	94	4.8
Gaura coccinea	83	0.4
Koeleria pyramidata	78	4.3
Carex eleocharis	78	2.3
Aristida longiseta	78	1.3

and signs of succession back to *Stipa/Carex* vegetation are now evident in numerous places. In Theodore Roosevelt National Park we also described the *Stipa comata/Carex filifolia* association. There it also occupies upland plateaus and gentle slopes (Hansen et al. 1984).

Stipa comata/Carex heliophila Habitat Type

This habitat type occurs in the western halves of the Sioux and Ashland Districts. It occupies upland plateaus or open parks surrounded by *Pinus ponderosa*. *Stipa comata* and *Carex heliophila* dominate the vegetation. *Artemisia ludoviciana, Koeleria pyramidata, Agropyron smithii* and *Stipa viridula* have high constancies and provide additional coverage (Table 2). Where the vegetation is disturbed, *Bromus japonicus, Artemisia frigida*, and in some cases, *Artemisia cana* and/or *Artemisia tridentata* may be abundant.

Festuca idahoensis/Carex heliophila Habitat Type

The *Festuca/Carex* association occurs along the western edge of the study region. It is quite extensive on upland plateaus or open parks surrounded by *Pinus ponderosa*. *Festuca idahoensis* dominates the vegetation and *Carex heliophila, Koeleria pyramidata, Artemisia ludoviciana, Aster ericoides* and *Agropyron smithii* provide additional coverage (Table 3). In disturbed stands (*Artemisia frigida* and *A. ludoviciana* become more abundant.

There is much similarity among the three plant associations described. The major differences in composition rest with very few species. *Festuca idahoensis* and *Stipa comata* trade places as dominants in two of these associations with some minor differences also apparent. The *Festuca/C. heliophylla* and *Stipa/C. heliophylla* associations also overlap in their distributions in the Ashland District. While the *Stipa/Carex* association occurs mainly on south- to southwest-facing slopes in the overlap area, the *Festuca/Carex* association occurs on all slopes in the same overlap area. The intermingling and overlap is not explained by the soil factors as the ones measured show no significant differences. Both associations in this area occur on loam to sandy loam soils that appear to be well-drained. Exchangeable cations, pH, and phosphorus, do not differ significantly between soils of these two habitat types. The *Stipa comata/Carex filifolia* habitat type is located somewhat east of the overlap areas.

MAJOR FOREST VEGETATION

Fraxinus pennsylvanica/Prunus virginiana Habitat Type

This habitat type occurs in upland ravines and broad valleys, on moderately steep slopes, and along small permanent or ephemeral streams throughout the study region. In each instance it is upland, not on the alluvial deposits of major stream courses, and it is categorized as a topographic climax.

The tree stratum is dominated by *Fraxinus pennsylvanica* with combinations of *Acer negundo, Ulmus americana, Juniperus scopulorum* and *Pinus ponderosa* also present in some of the stands. In sharply-cut, V-shaped upland ravines, the largest *Fraxinus* are near the center, or bottom, of the ravine where the soil moisture is greatest.

The undergrowth is dominated by *Prunus virginiana*, 2-3 m tall (Table 4). *Carex sprengelii* and *Elymus virginicus* dominate the herbaceous layer. Along the fringes of these stands, *Prunus* frequently forms dense ecotonal thickets before giving way to steppe higher on the slopes.

In stands relatively free of disturbance, the diversity of shrubs and forbs is high and abundant tree seedlings are present. Disturbance eliminates much of the shrub and forb vegetation and reduces tree seedling numbers dramatically. Browsing and/or trampling kills many of the younger trees. Severe disturbance reduces diversity and produces stands characterized by a few scattered older trees with no reproductions. Also, *Poa pratensis, Bromus inermis, Bromus japonicus, Melilotus officinalis*, and *Symphoricarpos occidentalis* increase with disturbance.

Only a limited number of relatively undisturbed stands of steppe or forest remain in this region. Their value to science is too important to permit complete alteration. Lack of understanding of rather basic ecological principles appears to be leading toward the eventual total destruction of the *Fraxinus*-dominated upland forests, given the overgrazing continues. The upland steppe vegetation appears to be somewhat more resilient to grazing. Species such as *Bouteloua gracilis* increase and withstand considerable grazing pressure. Still, there should be preserved examples of the vegetation in climax or near-climax condition to provide the opportunity for further study. Only a few of the questions about this resource have been answered, and fewer have been asked.

TABLE 2. Constancy and mean coverage of shrubs, graminoids and forbs that attain a constancy of 80% or more in the *Stipa comata/Carex heliophila* habitat type. Values are based on data of 10 stands.

Species	Constancy	Mean Coverage
Stipa comata	100%	61.5%
Carex heliophila	100	48.3
Artemisia ludoviciana	100	6.2
Koeleria pyramidata	100	5.1
Agropyron smithii	100	4.9
Stipa viridula	90	5.5
Antennaria rosea	90	0.8
Gaura coccinea	90	0.2
Aster ericoides	80	1.7
Artemisia frigida	80	1.4
Psoralea argophylla	80	0.3
Echinacea angustifolia	80	0.2

TABLE 3. Constancy and mean coverage of shrubs, graminoids and forbs that attain a constancy of 75% or more in the *Festuca idahoensis/Carex heliophila* habitat type. Values are based on data of 8 stands.

Species	Constancy	Mean Coverage
Festuca idahoensis	100%	75.3%
Carex heliophila	100	25.5
Koeleria pyramidata	100	4.0
Artemisia ludoviciana	100	2.8
Aster ericoides	100	2.7
Agropyron smithii	100	2.6
Stipa comata	88	2.6
Rosa arkansana	75	0.8
Stipa viridula	75	0.4
Bromus japonicus	75	0.3
Antennaria osea	75	0.3
Artemisia frigida	75	0.3

TABLE 4. Constancy and mean coverage of shrubs, graminoids and forbs that attain a constancy of 75% or more in the *Fraxinus pennsylvanica/Prunus virginiana* habitat type. Values are based on data of 14 stands.

Species	Constancy	Mean Coverage
Carex sprengelii	100%	33.7%
Prunus virginiana	93	53.9
Elymus virginicus	86	13.8
Smilacina stellata	86	2.7
Galium aparine	79	6.1

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THE MANY FACES OF SOUTH DAKOTA RANGELANDS: DESCRIPTION AND CLASSIFICATION

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Abstract. Most rangeland in South Dakota is a Mixed Prairie grassland comprised of a mosaic of varied plant communities. Only a few scattered tracts of Tallgrass Prairie occur in the extreme eastern portion of the state. The Shortgrass Prairie does not occur, and forestland is found mostly in the Black Hills. Even with massive conversions of rangeland to cultivated land, rangeland still dominates the South Dakota landscape.

The terms rangeland and grassland are synonymous in the language of some members of the scientific community. Range implies a kind of land rather than a use of land, further cementing its identity with grassland. In this paper, prairie will refer to the remnant Tallgrass area of South Dakota, most of which is rangeland used by livestock and wildlife.

Broad expanses of rangeland across South Dakota may appear homogeneous to most travelers following modern highways; yet, there are many forms of the Mixed Prairie due to variations in environmental conditions. Some communities exhibit varying degrees of retrogression from their potential due to the activities of man. Management of animals utilizing native rangelands is critical to maintain vegetation in its most productive state. Range managers promote plant welfare and in this sense share a common interest with others who have an interest in grassland ecosystems.

INTRODUCTION

Knowledge of the potential natural vegetation of any geographic area is of utmost importance to those who use and manage vegetation. The vegetation of the Northern Great Plains is predominantly grassland, woody plants exerting dominance only in local areas. Even in its present fragmented form, this grassland is one of the most productive ecosystems in North America and, perhaps, in the world.

Rangeland is defined as land on which the native vegetation is predominantly grasses, grass-like plants, forbs, or shrubs suitable for grazing or browsing by domestic or wild animals (Society for Range Management 1974). Clearly, the term "range" refers to a kind of land rather than a use of land. The range or grassland remaining in South Dakota today is a Mixed Prairie, most of the Tallgrass Prairie having disappeared beneath the plow many decades ago. Identifying the potential natural vegetation was important for assuring proper management of this vast range resource. Schumacher (1975) noted the extent of the prairie (rangeland) in the Dakotas, Nebraska, Minnesota, and Iowa at an earlier prairie conference. He discussed the range management principles and practices that apply to the use and management of this vast ecosystem. While climate, geologic parent material, soils, and vegetation do not conform to political boundaries, the following discussion will, nevertheless, be limited to South Dakota.

TOPOGRAPHY, PHYSIOGRAPHY, CLIMATE

South Dakota, located in the geographical center of North America, also lies within the large region known as the Grassland Province. Elevation generally increases from about 275 to 460 m (900 to 1,500 ft) along the eastern border to 915 to 1,070 m (3,000 to 3,500 ft) along the western border. The highest point in the United States east of the Rocky Mountains is Harney Peak in the Black Hills at 2,208 m (7,241 ft) elevation.

The major portion of the state lies within the Great Plains physiographic province, and a smaller portion in the Central Lowlands Province (Denson 1964). The Great Plains Province is a broad highland that slopes gradually eastward from the Rocky Mountains on the west to the Central Lowlands on the east (Fig. 1). That portion of the Great Plains Province in the western two-thirds of South Dakota has been termed the Missouri Plateau by some authors. The Central Lowlands Province extends from the drainage basin of the James River (approximately the 99th Meridian) eastward.

All attributes of South Dakota's climate are highly variable, with long-term precipitation perhaps best exemplifying that variability. The capital city, Pierre, is located near the center of the state just west of the 100th Meridian, the arbitrary border between the subhumid and semiarid climatic zones. Schumacher (1974) analyzed the 81-year Pierre precipitation record, 1892-1972, and noted that, according to Thornthwaite's (1936) climatic classification scheme, five of the years were arid, 33 semiarid, 31 dry subhumid, 12 moist subhumid, and none were humid. Wet and dry years tended to be grouped. Dry years can be quite severe,

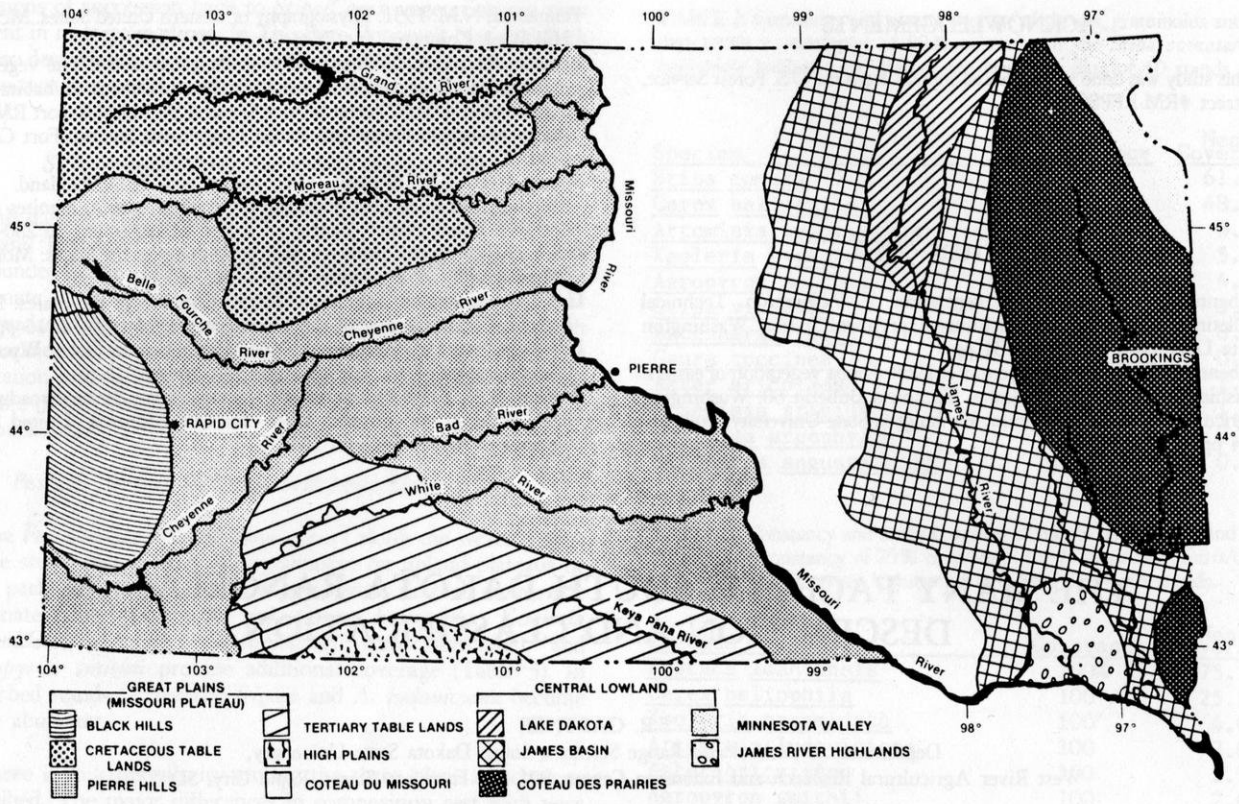

FIG. 1. Major physiographic divisions of South Dakota.

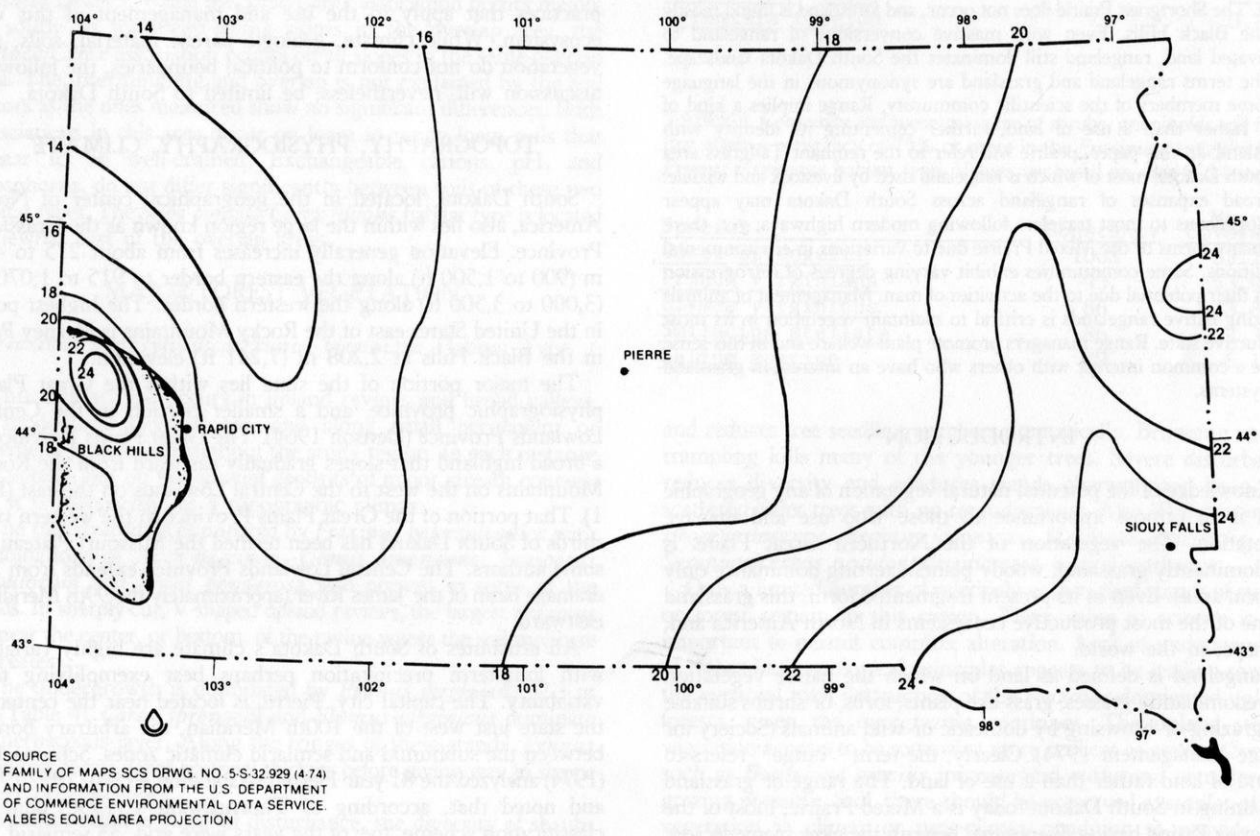

FIG. 2. South Dakota average annual precipitation (inches) 1941-70.

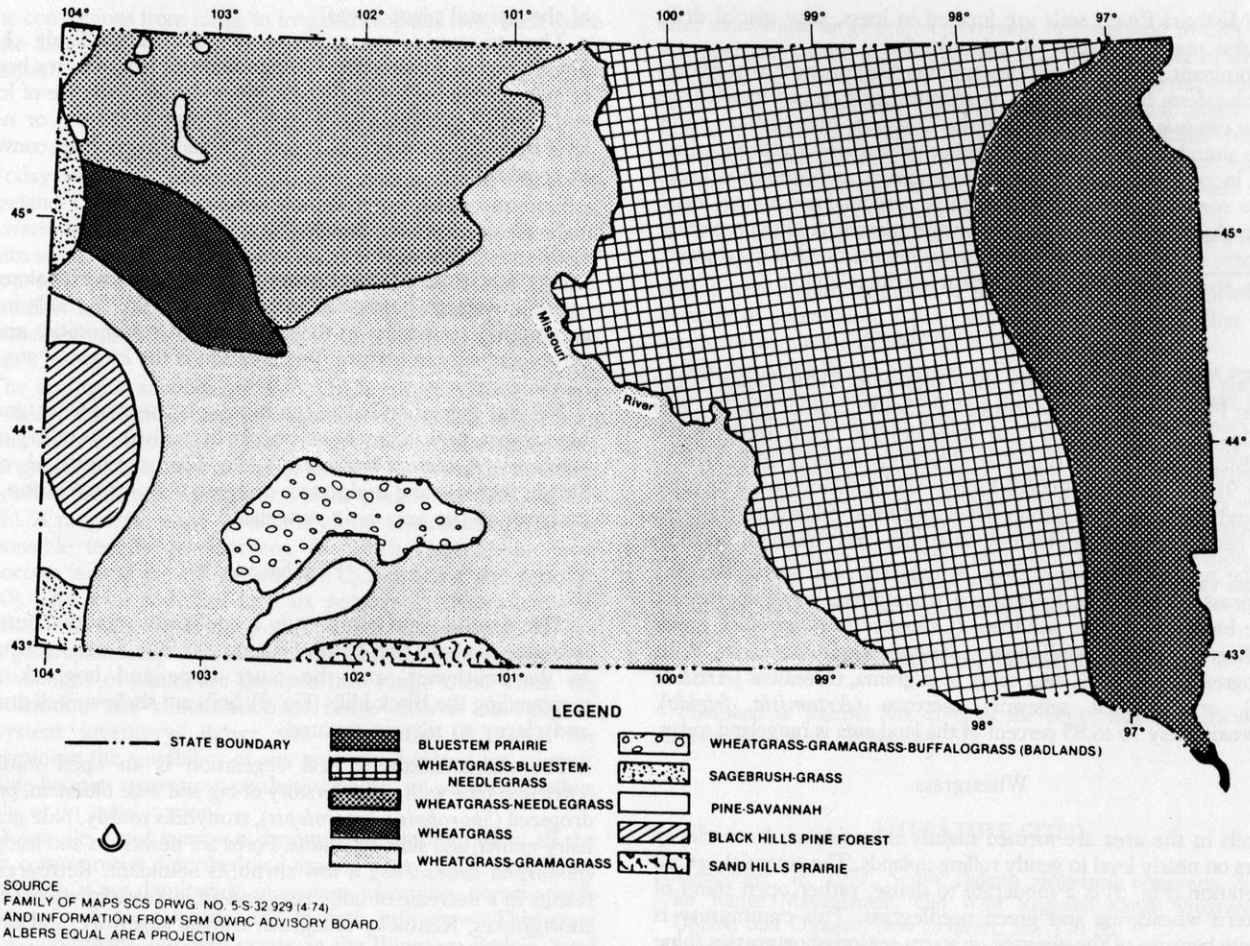

FIG. 3. South Dakota natural vegetation.

especially when spring and early summer precipitation is deficient. Plant moisture stress (drought) seems to occur somewhere in the state nearly every year.

Annual precipitation increases from about 330 mm (13 in) in the northwest corner of the state to about 660 mm (26 in) in the southeast (Fig. 2). About 75 percent occurs during the growing season, April through September. Note that the 18-inch (457 mm) precipitation isohyet nearly conforms to the 100th Meridian and the eastern boundary of the Great Plains Province (Figs. 1 and 2).

SOUTH DAKOTA NATURAL VEGETATION

A map of the pre-settlement or potential natural vegetation of South Dakota was developed in 1976 by the Soil Conservation Service with assistance from several plant ecologists in the state (Baumberger 1977). The map (Fig. 3), embracing some of Küchler's (1964) vegetation types, reveals that nearly all the land area of the state was once grassland. Other ecosystems occurring included the ponderosa pine forest in the Black Hills and a small portion of sagebrush grassland along the western border. Characteristic vegetation, soils, range sites, distribution, uses, and suggested livestock carrying capacities of each community were detailed by Baumberger (1977). Brief descriptions of each plant community are reported herein.

Bluestem Prairie

This tallgrass community once occupied most of the extreme eastern edge of South Dakota on what is known as the Prairie Coteau (Figs. 1 and 3). The general aspect, in a pre-settlement state, consisted of a dense cover of tallgrasses and an abundance of showy forbs. Soils are deep and formed mainly in glacial drift or loess. Elevations range from a low of about 275 m (900 ft) above sea level in the extreme northeast corner of the state to about 457 m (1,500 ft) in the southeast corner. Dominant species of this portion of the Tallgrass Prairie are big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), porcupine grass (*Stipa spartea*), and tall dropseed (*Sporobolus asper*). With retrogression, species increasing in abundance include western wheatgrass (*Agropyron smithii*), sideoats grama (*Bouteloua curtipendula*), blue grama (*B. gracilis*), hairy grama (*B. hirsuta*), and buffalograss (*Buchloe dactyloides*). Further retrogression in condition allows exotics, such as Kentucky bluegrass (*Poa pratensis*), to invade.

Today, probably 70 to 85 percent of this area is in cropland. What remains of the Bluestem Prairie is mostly in low range condition with a high percentage of exotics and other invader species. Some Bluestem Prairie areas have recently been restored and are being maintained with periodic fire to control invaders and stimulate native species.

Wheatgrass - Bluestem - Needlegrass

The characteristic vegetation of this community is a dense cover of tall and midgrasses. It occupies the transition between the Mixed and Tallgrass Prairies in three major physiograhic divisions (Figs. 1 and 3).

Soils are mostly deep, having formed in glacial till or loamy glacial drift on uplands. At the western edge of the area and along

the Missouri River, soils are formed in loess, silty glacial drift, or loess mantled glacial till on uplands.

Dominant species in pristine condition were western wheatgrass, big bluestem, little bluestem, porcupine grass, green needlegrass (*Stipa viridula*), and prairie junegrass (*Koeleria pyramidata*). Forbs were abundant. The altered community develops a shorter aspect with increases in sideoats grama, blue grama, and needleandthread (*Stipa comata*), as well as less desirable perennial and annual forbs. Kentucky bluegrass is a common invader species. A high percentage (perhaps 60-70 percent) of this area has been converted to cropland. Only steep and rocky soils remain as rangeland.

Wheatgrass - Needlegrass

This community occupies the Cretaceous Table Lands of the Great Plains Province in northwestern South Dakota (Fig. 1). Soils in this area are shallow and were formed from sedimentary sandstones and sandy shales at elevations ranging from 610 to over 915 m (2,000 to 3,000 ft) above sea level. Soils are a mixture of sandy and loamy materials developed from calcareous deposits, and residuum from sandstones, siltstones, and shales on uplands.

The natural vegetation (Fig. 3) consists of a dense cover of midgrasses dominated by western wheatgrass, needleandthread, little bluestem, prairie sandreed (*Calamovilfa longifolia*), green needlegrass, and stonyhill muhly (*Muhlenbergia cuspidata*). With retrogression, sedges (*Carex* spp.), blue grama, threeawns (*Aristida* spp.), and fringed sagewort increase (*Artemisia frigida*). Approximately 75 to 85 percent of the land area is rangeland today.

Wheatgrass

Soils in the area are formed mainly in residuum from clayey shales on nearly level to gently rolling uplands. The potential natural vegetation (Fig. 3) is a moderate to dense, rather open stand of western wheatgrass and green needlegrass. This community is unique because of the absence of warm-season shortgrasses (blue grama and buffalograss) in the understory on Dense Clay range sites. Retrogression of the community is characterized by reduced midgrass cover and increases in cactus species (*Opuntia* spp.), annual saltbushes (*Atriplex* spp.), common sunflower (*Helianthus annuus*), and other forbs. Only a small percentage (probably less than five percent) of this area is cultivated because of soil and precipitation limitations.

Wheatgrass - Gramagrass

This area is underlain by the Pierre shale formation at elevations of about 550 to about 850 m (1,800 to 2,800 ft) above sea level (Fig. 1). Soils were formed mainly in residuum from clayey or silty shales on uplands.

A moderately dense stand of mid and shortgrasses characterizes the natural vegetation (Fig. 3). Dominants are western wheatgrass and green needlegrass with an understory of blue grama and threadleaf sedge (*Carex filifolia*). Perennial forbs are abundant. With retrogression, the midgrasses decrease in abundance and blue grama, buffalograss, and cactus species increase. Common invaders in this community are Japanese brome (*Bromus japonicus*), and curlycup gumweed (*Grindelia squarrosa*). Conversion of range to cropland has taken place at a rapid rate in the community in recent years and soil erosion has become a major problem.

Wheatgrass - Gramagrass - Buffalograss (Badlands)

The natural vegetation of the Badlands area (Fig. 3) includes both the midgrasses and shortgrasses previously mentioned. Sideoats grama and little bluestem are abundant on shallow soils of slopes. Rocky Mountain juniper (*Juniperus scopulorum*) and ponderosa pine (*Pinus ponderosa*) are found on some sites. The shortgrasses, needleandthread, and dryland sedges increase with deterioration of the natural plant cover.

The vegetation occupying the Tertiary Table Lands physiographic division (Fig. 1) has a wide variety of forms because of extreme variability in topography and soils. Soils are of loamy and clayey texture and located on either steep slopes or nearly level lands. Only a very small portion of the area has been converted to cropland.

Sagebrush - Grass

The Sagebrush - Grass community occurs primarily along the extreme western border of South Dakota (Fig. 3). Soils in this community are similar to those of adjacent communities and are clayey and silty in texture. Precipitation is the lowest of any area in the state.

Natural vegetation in the community consists of wheatgrasses, blue grama, prairie junegrass, and forbs, with an overstory of big sagebrush (*Artemisia tridentata*) and/or silver sagebrush (*A. cana*). Shrubs increase and midgrasses decrease with retrogression. The majority of the area is in rangeland.

Pine Savannah

This natural plant community is confined to wooded buttes in extreme northwestern South Dakota, the Pine Ridge escarpment in the southwest, and the outer slope and hogback ridge surrounding the Black Hills (Fig. 3). Soils are shallow, well-drained, and clayey to silty in texture.

The characteristic natural vegetation is an open stand of ponderosa pine with an understory of big and little bluestem, prairie dropseed (*Sporobolus heterolepis*), stonyhills muhly, blue grama, hairy grama, and sideoats grama. Forbs are numerous and leadplant (*Amorpha canescens*), a low shrub, is abundant. Retrogression results in a decrease of tallgrasses and an increase in warm-season shortgrasses, Kentucky bluegrass, fringed sagewort, and broom snakeweed (*Gutierrezia sarothrae*). Western wheatgrass also increases on some sites. Ponderosa pine has increased dramatically, especially in the foothills of the Black Hills, probably because fire suppression has been nearly complete over the past 75 to 100 years. Deciduous trees and shrubs commonly occupy drainages. Land conversions in this community are from range to housing and recreation developments in the foothills of the Black Hills.

Black Hills Pine Forest

The natural vegetation consists of open to dense ponderosa pine forest with a diverse understory of shrubs and herbaceous plants (Fig. 3). Within the pine forest are numerous, rather large grassland areas with a rich flora. Retrogression is characterized by increased density of pine with decreasing diversity in the understory, probably a result of fire exclusion over many decades. The demand for sawlogs and pulpwood is inadequate to keep pace with the reproduction and growth rate of ponderosa pine in the Black Hills. Housing, recreation developments, roads, and mining have reduced the available area of forest-rangeland for both domestic livestock and wildlife.

Sand Hills Prairie

This community occupies the northern edge of the Nebraska Sand Hills from 915 to 1,100 m (3,000 to 3,600 ft) elevation (Fig. 3). Soils are mostly deep, undulating to rolling, and sandy textured.

The natural plant cover includes little bluestem, big bluestem, sand bluestem (*Andropogon hallii*), prairie sandreed, needleandthread, sideoats grama, western wheatgrass, and a wide variety of forbs. Leadplant, wild rose (*Rosa* spp.), sand cherry (*Prunus besseyi*), and yucca (*Yucca glauca*) are locally abundant. With retrogression, tallgrasses yield to shorter species, and sand sage (*Artemisia filifolia*) and sageworts (*Artemisia* spp.) increase.

Some conversions from range to irrigated cropland have been made in the Sand Hills where sufficient water is available from wells or other sources.

SUMMARY AND DISCUSSION

Today about 50 percent of the land area of South Dakota is rangeland. Cool-season grasses dominate most plant communities, but warm-season shortgrasses, sedges, and forbs are also abundant. Shrubs are not dominant except in the Sagebrush-Grass community and a few local areas. Identification of the potential natural vegetation has provided a yardstick for determining optimum livestock carrying capacity for the various kinds of rangeland in South Dakota.

The ecological subdivisions into which rangelands are divided for study, evaluation, and management are called range sites (Schumacher and Johnson 1980). A range site is a distinctive kind of rangeland that differs from other kinds of rangeland in its ability to produce a characteristic natural plant community (USDA, SCS 1976). A range site is the product of all the environmental factors responsible for its development. In South Dakota, the most important factors are climate and soil (Schumacher and Johnson 1980). The state is divded into six geographic areas each with distinctive climatic features, especially annual precipitation. Within each geographic area, soils that have the potential to produce similar combinations of plants are grouped into range sites. Thus, the identification and classification of range sites is basically an ecosystem inventory. Range site information is useful for determining the suitability of any area of rangeland for grazing, wildlife habitat, recreation, aesthetic quality, or watershed value, singly or in combination.

The single, most common denominator among nearly all the plant communities described and among many range sites is the occurrence, if not dominance, of western wheatgrass across a wide variety of soil, topographic, and climatic influences. This grass is not a dominant, but does occur, in the Bluestem Prairie, Sand Hills Prairie, Pine Savannah, and Black Hills Pine Forest communities. Western wheatgrass, by virtue of its ability to survive and reproduce by rhizomes, has withstood plowing, prolonged drought, flooding, overgrazing, overseeding, and fire. Today, western wheatgrass is recognized as the key management species on many range sites.

Several factors led to retrogression in the majority of South Dakota grasslands. The free-roaming native grazers, especially the bison, were eliminated and were replaced by domestic livestock. Settlement followed, and homesteading was synonymous with the plow. Settlement also necessitated fencing and, often, too many animals were enclosed on insufficient acres.

As the population grew, especially following World War II, demands for agricultural products led to more intensive land use. Surface mining, housing and highway development, industry, and other activities all contributed to higher land values. In recent years, higher small grain prices and subsidies resulted in escalating land values and large scale conversion of rangeland to cropland. As more acres were plowed, the pressure on remaining rangeland increased because livestock numbers were not correspondingly reduced to the carrying capacity of fewer grazable acres. The magnitude of retrogression from the natural or climax state is extremely variable throughout South Dakota. Large acreages of private and public rangeland are being maintained at or near their potential with superior range management.

Only history will record whether or not South Dakota's range resources can withstand current pressures. Thousands of tons of topsoil have already been lost to wind and water erosion, primarily because of conversions from rangeland to cropland. What took centuries to construct has been lost in a decade or so.

The future of Range Science and Range Management is replete with challenges on South Dakota's present and former rangelands. As small grain yields and prices decrease, many landowners will request assistance in converting cropland back to grassland. The era of the "vanishing prairie" may provide the greatest challenge for future range managers, ecologists, and other specialists in the plant and soil sciences. The unique quality that makes rangeland so valuable is that the major product - native vegetation - is renewable each growing season without the cost of energy inputs, fertilizers, and labor associated with farming practices.

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Part 4. ANIMAL LIFE ON THE PRAIRIES

RAILROAD GRASSLANDS AS BIRD AND MAMMAL HABITATS IN CENTRAL IOWA

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Abstract. Populations and habitat associations of birds and mammals were evaluated for one year on five percent of the railroad rights-of-way (ROWs) in Story County, Iowa. Twenty percent of the nongrazed, unmowed grassland habitats in the county occurred on railroad ROWs. Coverage of native prairie vegetation on the study plots averaged 36 percent. Bird diversity and density were less in herbaceous ROWs than in woody ROWs, but the opposite tended to be the case for mammals. Alien grass species were more common (averaging 58 percent of a study plot) than native species. Negative correlations existed between bird diversity and alien grass coverage, while positive correlations existed between small mammal diversity and alien grass coverage. Some grassland bird species made little use of railroad ROWs. Locally scarce mammals which utilized the ROWs included grassland species which was not the case for birds. At least four mammal species utilized the railroads as travel corridors.

Railroad rights-of-way are among the few areas of permanent vegetation left in much of the intensively agricultural midwestern United States. Many railroad lines are being abandoned and rapidly converted to cultivated land. To help document the value of these areas to wildlife, I investigated the use of rural railroad ROWs by birds and mammals in Story County, Iowa.

STUDY AREA AND METHODS

Story County is typical of intensively farmed central and northern Iowa, and intensive land use studies of the county have been done (Anderson et al. 1975, Taggart 1974). Twenty study plots within the county were selected by a stratified random design. The two major strata were active and abandoned railroad ROWs. Each plot occupied the width of the ROW (typically 30.5 m), and all but one were 0.4 km in length (typical plot area was thus 1.2 ha). The exception was approximately 92 m wide and 152 m long, and the change was made because of the unusually large ROW width. Collectively, the 20 plots comprised approximately 5 percent of the rural railroad ROW mileage in the county.

Vegetation on the study plots was evaluated by cover mapping. Vegetational patches were outlined on a map of the plot, and the common plant species of each patch were identified but not quantified. Vegetation percentages on each plot were calculated using a grid overlay on the cover maps (Braband and Klaas 1981). Vegetational cover types of the land adjacent to the plots and the amount of snow cover on the plots were also recorded.

The bounded count method (Robson and Whitlock 1964) was used to estimate population densities for bird species seen on the plots. On each count, the researcher walked through the plot and recorded on a copy of the vegetation cover map the species and location of each bird observed. Aerial-foraging birds, such as swallows, were also recorded. Since differences in time spent counting can bias the number of birds observed, efforts were made to spend approximately 45 min in each plot during a count. Five or six counts (replicates) per plot were obtained in each sampling period. Since bird activity varies with the time of day, replicate counts on each plot were relatively evenly distributed throughout the day. The Shannon diversity and species richness indices (Poole 1974) were calculated for the bird communities of each plot for every census period.

Small mammal populations were assessed by snaptrapping during autumn when numbers for most species were probably high. Methods generally followed those described by Smith et al. (1975). Trapping stations were placed approximately 15 m apart with 12 stations per sampling plot along a line roughly parallel to the tracks. Two museum specials and one regular-sized snaptrap were placed at each trapping station. Except on three plots, the side of the tracks to be trapped was decided by a coin-flip. The exceptions included two plots where one side of the tracks was avoided because of a narrow ditch. In a third case, one side of the plot was selected to sample an exceptionally good stand of native prairie. Traps were set for a five-day period and checked daily.

Accurate estimates of small mammal density require more sophisticated approaches than my trapping design (Smith et al. 1975). Thus, the results of this study's small mammal trapping are considered as relative rather than absolute measures of density. The Shannon diversity and species richness indices (Poole 1974) were calculated for the small mammal communities of each plot.

Rabbits in each plot were censused simultaneously with the bird counts using the bounded count method.

Presence of ground squirrels was determined by livetrapping during summer. Four livetraps (46 x 38 x 38 cm) were placed about 46 m apart on each plot. Each trap was baited with bacon, lettuce, and rolled oats. Unless already shaded, the traps were partially covered with herbaceous vegetation cuttings. The traps were tied open and baited for several days. Actual trapping was done during daylight hours over a three- or four-day period. Traps, when set, were checked about each hour. Ground squirrels captured were toe-clipped for later identification and released.

Plains pocket gopher populations were estimated on each study plot by counting the number of sets of fresh mounds and assuming one gopher per each set of mounds (Mielke 1977, Reid et al. 1966).

Dens, droppings, trails, and other signs of mammal activity on the plots were recorded in the course of other field work.

Scientific names of bird and mammal species referred to are in the Appendix.

Vegetation cover maps were made during summer 1977 and rechecked during summer 1978 for phenological changes. Bird and mammal censuses were initiated in September 1977 and continued through August 1978. Bounded counts were run from October 8 - November 19 (fall), January 2 - February 5 (winter), March 6 - April 2 (early spring), April 3 - April 30 (midspring), May 2 - May 30 (late spring), and June 5 - July 4 (summer). Small mammals were trapped from September 27 - October 30, while ground squirrels were trapped from July 11 - August 9. Pocket gopher censusing was conducted from May 23 - June 24.

Data were analyzed on an ITEL AS-6 computation system using SAS programming (Barr et al. 1976) and on a Franklin ACE 1200 microcomputer using programming prepared by the Educational Computing Section of Chelsea College, London (Leveridge 1979).

Analysis of variance, Duncan's multiple range tests, and student t-tests were used to determine statistical differences of bird diversity indices and bird densities versus habitat types. Pearson's correlation coefficients were calculated for diversity indices and bird densities versus land use adjacent to the plots and the amount of shrubs, trees, alien grass, native grass, and annual forbs in the plots. One-way analysis of variance and least squares tests were calculated on the diversity indices and bird densities versus the habitat types, snow cover, ROW width, train activity, and number of shrubs and trees. In any census period, only bird species which occurred on at least 20 percent of the study plots were statistically tested. Level of significance for all tests was $P \leq 0.05$.

Duncan's multiple range, student t-tests, Pearson's correlation coefficient, one-way analysis of variance, and least squares tests were run on the small mammal diversities and densities, cottontail and gopher densities, and winter mammal track frequencies versus the same factors as used in the bird analyses. Level of significance for all tests was $P \leq 0.05$.

Since much of the data were discrete units, a portion was transformed to more closely fit a normal distribution. These transformed data were then statistically analyzed and compared to the analysis of the original data. Few differences occurred, thus the statistical results presented were with the untransformed data.

RESULTS AND DISCUSSION

General Trends

Over 90 percent of Story County lacks suitable wildlife cover, especially in winter and early spring (Anderson et al. 1975, Taggart 1974). About 4 percent of the county's grassland occurs on railroad ROWs (Table 1). However much of the permanent grass habitat is either heavily grazed pasture or frequently disturbed narrow ditches along county highways. Excluding these, railroad ROWs contain an estimated 20 percent of the permanent grass habitat of the county. Coverage of native prairie (including wetland) vegetation on the study plots varied from 4 to 78 percent with an average of 36 percent. By extrapolation, 81 percent of the prairie remnants in rural Story County occurred on railroad ROWs (Braband and Klaas 1981).

Study plots were classified according to three habitat types based on results of the grid-overlay analysis of the cover maps (Table 2). Two types (grass and grass-annual forb) were dominated by herbaceous vegetation, while the remaining type (shrub/woodland) had at least 10 percent (range of 11 to 42 percent) of each plot occupied by woody growth.

Bird diversities were higher in the woody plots than in the herbaceous plots (Table 3). Bird densities were also generally higher in the woody plots (Table 4). Only the Horned Lark, House Sparrow, and Vesper Sparrow regularly occurred at higher densities in the herbaceous habitats (Braband 1979). The presence of House Sparrows may have been influenced more by the proximity of buildings and other structures than by vegetational characteristics. The Western Meadowlark and Dickcissel did not show a strong preference for either the herbaceous or woody plots (Braband 1979) probably because 4 out of the 6 woody habitat plots also contained much open grassland.

During the breeding (summer) census period, 33 bird species occurred on herbaceous plots. A total of 22 species of birds were either confirmed or probable breeders within the herbaceous ROW plots (Table 5). Of these, 9 species nested on the ground or in low herbaceous vegetation, while the remaining 13 nested in isolated trees, shrubs, human-made structures, or other bird nests within the ROW. The most common breeding species within the herbaceous plots were the House Sparrow, Red-winged Blackbird, Song Sparrow, Common Yellowthroat, Brown-headed Cowbird, Vesper Sparrow, and Dickcissel. The Barn Swallow and Common Grackle were common foragers within the plots. American Goldfinches were also common, but the summer census period was before most of the species nest.

TABLE 1. The relative value of railroad ROW grasslands in Story County, Iowa.

Habitat	Rural Area (ha)	Area on Railroad ROWs (ha)	Percent
TOTAL COUNTY	144,066	622	less than 1
Grassland (all)	9,593	432	4
Grassland (ungrazed, unmowed[a])	2,133	432	20

[a] Excludes areas which are frequently disturbed, especially by heavy grazing and mowing.

TABLE 2. Vegetative cover found on railroad ROW study plots with each assigned to one of three habitat types.

Vegetative Classes	Habitat Types[a] Grass (7)	Grass-annual(7)	Shrub/Woodland(6)
Alien grasses	55.6	72.2	43.5
Native grasses	36.4	35.5	33.2
Annuals[b]	11.2	33.5	34.4
Forbs[c]	15.2	9.0	8.0
Shrubs	1.6	1.2	17.6
Trees	0	0	7.4
Wetland	1.6	1.0	1.8
Barely vegetated	20.4	7.8	9.6
Other	14.0	17.4	11.0

[a]The number of plots in each habitat type is in parentheses. Values represent averages of percent areal coverage of each vegetative class relative to total plot area.
[b]Annuals are largely early successional nongrass herbs.
[c]Forbs are largely nongrass herbs not typical of early succession.

During the autumn and spring census periods, a total of 50 migrant bird species occurred on herbaceous ROW plots. The most common migrants on herbaceous plots were the Red-winged Blackbird, Song Sparrow, Dark-eyed Junco, Brown-headed Cowbird, American Robin, Vesper Sparrow, American Tree Sparrow, Western Meadowlark, Barn Swallow, Savannah Sparrow, Common Grackle, and Brown Thrasher (Table 5). Habitat analysis revealed that the amount of shrubs, trees, and annual forbs appeared important in determining the use of the plots by many migrants (Braband 1979). This was especially evident with sparrows, such as the Fox Sparrow and White-crowned Sparrow, which typically frequent shrubby areas (Austin 1968). In contrast, the Savannah Sparrow occurred more often on ROWs which lacked trees. The Le Conte's Sparrow was usually flushed from tall, relatively rank grassy vegetation. Austin (1968) stated that, in migration, Le Conte's Sparrows prefer wetter grass. All of my study plots containing this species were either located in lowland areas or contained low, wet spots.

During the winter census period, 13 bird species occurred in the herbaceous plots. The most common birds in the herbaceous ROW plots were the Snow Bunting, House Sparrow, and Ring-necked Pheasant (Table 5). The Snow Bunting occurred only in the herbaceous plots, however its distribution was irregular and clumped. Often the species was present in large numbers on a plot during one replication and absent the next. Ring-necked Pheasants largely occurred as flocks centered in patches of shrubby vegetation.

The woody railroad ROWs had slightly more mammal species (12.3 species per plot) than the herbaceous (11.4 species per plot).

TABLE 3. Bird species diversity and richness on railroad ROWs in Story County, Iowa, 1977-1978, by census period and habitat type.

Habitat	N	Census Period[a]											
		Fall		Winter		Early Spring		Mid-Spring		Late Spring		Summer	
Shannon index:													
Herbaceous plots	14	0.641	(0.225)	0.181	(0.255)	0.416	(0.268)	0.844	(0.149)	0.931	(0.166)	0.990	(0.126)
Woody plots	6	0.966	(0.182)	0.584	(0.321)	0.845	(0.157)	1.066	(0.163)	1.219	(0.268)	1.267	(0.093)
Species richness:													
Herbaceous plots	14	*7.0	(3.3)	*2.1	(1.8)	*4.1	(2.3)	*8.9	(2.4)	*10.8	(3.8)	*12.4	(3.7)
Woody plots	6	*17.5	(4.0)	*6.5	(4.0)	*11.5	(4.4)	*16.7	(4.2)	*26.2	(8.4)	*24.3	(4.3)

[a]Average values for each census period are based on the number of plots (N) in each habitat type; standard deviations are in parentheses. In any one census period, asterisked means are significantly different (two-tailed Student-t test, $P \leq 0.05$).

TABLE 4. Bird species density on railroad ROWs in Story County, Iowa, 1977-1978, by census period and habitat type.

Habitat	N	Census Period[a]											
		Fall		Winter		Early Spring		Mid-Spring		Late Spring		Summer	
Total density[b]													
Herbaceous plots	14	*63.8	(53.5)	*84.0	(117.9)	*31.4	(34.4)	*36.4	(15.6)	*39.5	(14.6)	*48.4	(19.1)
Woody plots	6	*173.0	(79.0)	*53.5	(40.1)	*99.8	(53.8)	*84.8	(23.3)	*120.8	(55.6)	*107.3	(31.5)
Density per species[c]													
Herbaceous plots	14	9.1	(6.4)	*62.6	(115.0)	6.4	(4.3)	4.1	(1.3)	3.7	(0.8)	3.9	(1.0)
Woody plots	6	9.7	(3.4)	*8.6	(3.6)	8.3	(3.7)	5.3	(1.6)	5.1	(3.0)	4.4	(1.0)

[a]Average values for each census period are based on the number of plots (N) in each habitat type; standard deviations are in parentheses. In any one census period, asterisked means are significantly different (two-tailed Student-t test, $P \leq 0.05$).

[b]Summation of bounded count estimates of all bird species on each plot.

[c]Total density divided by number of species on each plot.

An evaluation of trends of abundance (Table 6) revealed an apparent trend for slightly higher density in herbaceous plots. Of the 22 species quantitative measurements were collected from, 11 species were more common in herbaceous ROWs, 8 were more common in the woody ROWs, while 3 species did not display a preference for either habitat type. Probably the most reliable diversity measurements were of small mammals which had higher (but not significantly so) Shannon and species richness indices in the herbaceous plots (Table 7).

Comparative Effects of Alien and Native Grasses

Coverage of alien grass species ($\bar{x}$ = 58 percent) on the study plots was greater than native ($\bar{x}$ = 36 percent) (Table 2). No clear statistical associations between native grass coverage and bird and mammal populations were evident. However, some alien grass associations were displayed.

The number of bird species was negatively correlated in the fall ($r = -0.47$, $P = 0.05$) and early spring ($r = -0.52$, $P < 0.05$) census periods with the amount of alien grasses. In contrast, the small mammal Shannon index was positively correlated ($r = 0.48$, $P = 0.03$) and meadow vole numbers were weakly positively correlated ($r = 0.43$, $P = 0.06$) with alien grass coverage on the plots. These grasses often formed thick mats which are attractive to many small mammals (Burt 1946, Thompson 1965). However, the lack of vegetative diversity may have reduced the value of alien grass stands for birds.

Comparisons of ROW Habitat with Adjacent Habitats

Bird and mammal use of the railroad ROWs was often related to the adjacent land use. For example during the winter, bird species richness was associated ($r = -0.66$, $P < 0.01$) with a lack of deep, drifted snow. The amount of drifted snow on the ROW was not only negatively correlated with the number of trees ($r = -0.52$, $P < 0.02$) and shrubs ($r = -0.62$, $P < 0.01$) on a plot but also positively correlated with the amount of plowed land ($r = 0.46$, $P = 0.05$) adjacent to the plot.

Some species displayed interesting contrasting uses of ROW and adjacent habitats. In winter, large flocks of Snow Buntings frequented the study plots with the center of foraging activity being on the ROW. The Horned Lark, in contrast, was often seen in large flocks on adjacent bare land but only rarely on the ROWs during winter.

Two grassland species, the Grasshopper Sparrow and Bobolink, were essentially absent from the railroad ROWs during the breeding season. However, they were often observed in Story County pastures and hayfields including some adjacent to study plots. The Grasshopper Sparrow has been recorded as a common nester in meadow and small grain strips narrower than railroad ROWs (Good and Dambach 1943). This species has also been reported as usually occupying habitats with a lack of litter accumulation (Austin 1968, Birkenholz 1972, Graber and Graber 1963, Wiens 1969). Perhaps too much litter occurred in railroad ROWs for Grasshopper Sparrows to breed. Bobolinks, however, are associated with high, dense vegetation and litter accumulation (Joyner 1978, Wiens 1969). Illinois Bobolink populations dropped 90 percent in ungrazed grasslands over a 50-year period (Graber and Graber 1963). The acreage of ungrazed grassland only decreased by a third during this period. However, most of what remained was road and railroad ROW. Possibly, this species needs larger areas of grassland than are found in railroad ROWs. In Ohio, Bobolinks were more common in blocks of meadow than in meadow strips (Good and Dambach 1943).

TABLE 5. Densities of most frequently encountered bird species on herbaceous railroad ROWs in Story County, Iowa, 1977-1978.

Species	Census Period[a]					
	Fall	Winter	Early Spring	Mid-Spring	Late Spring	Summer
American Kestrel	0.1	0	0.1	0.5	0	0
Ring-necked Pheasant[b]	2.6[f]	2.7[f]	2.5	1.7	1.5	0.5[e]
Rock Dove	2.9[f]	3.1[f]	1.0	0.4	0.6	1.2
Mourning Dove[b]	1.9[f]	0	0	0	0.7	0.9
Cuckoo spp.[c]	0	0	0	0	0.1	0.9
Chimney Swift	0	0	0	0	0.6	0.5
Common Flicker	0.3	0	0.2	0.9	0	0.3
Red-headed Woodpecker	0	0	0	0	0.8	0.7
Downy Woodpecker	0.2	0	0	0.4	0	0.1
Eastern Kingbird[b]	0	0	0	0.1	0.7	1.1
Horned Lark[b]	0	0.6	1.6	1.0	0	0.3
Tree Swallow	0	0	0	0.8	0.1	0
Barn Swallow	0.3	0	0	0.6	3.0	5.0
American Crow	0	0	0.5	0.4	0.3	0.6
Brown Thrasher[c]	0	0	0	0.1	1.4	0.6
American Robin[b]	2.4	0	0.3	1.6	0.8	1.1
European Starling	0.1	1.3	5.9	1.0	0.3	0.9
Common Yellowthroat[c]	0	0	0	0	0.9	2.5
Dickcissel[c]	0	0	0	0	0.9	1.4
Savannah Sparrow	2.7	0	0	0.1	0.6	0
LeConte's Sparrow	0.9	0	0	0	0	0
Grasshopper Sparrow	0	0	0	0.7	0.4	0.1
Vesper Sparrow[b]	1.0	0	0	2.6	1.2	2.1
Dark-eyed Junco	7.8	0.4	1.8	2.2	0	0
American Tree Sparrow	3.5	0.7	0.9	0.1	0	0
Song Sparrow[b]	5.7	0	1.7	3.2	2.3	2.6
Snow Bunting	0	67.6[f]	0.6	0	0	0
Meadowlark spp.[b,d]	0.1	1.0[f]	0.7	1.6	1.8	0.6
Red-winged Blackbird[b]	0.4	0	2.4	4.5	6.4	6.1
Common Grackle[b]	0	0	0	0.5	1.5	2.9
Brown-headed Cowbird[b]	0	0	0	2.7	3.5	2.2
American Goldfinch[b]	4.0	0.1	0.1	0	0.9	1.9
House Sparrow[b]	19.2	5.9	10.6	5.4	5.1	6.8

[a] Values are averages of bounded count estimates made for each of 14 herbaceous study plots. Only species which occurred on at least 3 of the 14 plots for at least one census period are considered.

[b] Confirmed breeders (nests and/or eggs). Additional confirmed breeding birds on the herbaceous study plots were the Northern Bobwhite and Northern Oriole.

[c] Probable breeders (territorial behavior, largely limited to ROW, displayed). Additional probable breeding birds on the herbaceous study plots were the Gray Catbird and Indigo Bunting.

[d] Predominantly Western Meadowlark.

[e] May be inaccurate because of secretive nature of nesting hen pheasants.

[f] Predominantly one large flock on a single plot.

TABLE 6. Mammalian abundance values of railroad ROW study plots in Story County, Iowa, 1977-1978.

Species	Technique	Average Value[a]	
		Herbaceous Plots	Woody Plots
Masked shrew	Snap-trapping[b]	1.2 (1.8)	0.5 (1.2)
Short-tailed shrew	Snap-trapping	1.0 (1.2)	0.5 (0.5)
Western harvest mouse	Snap-trapping	2.5 (2.2)	1.5 (2.1)
Deer mouse	Snap-trapping	*9.3 (6.4)	*4.0 (4.4)
White-footed mouse	Snap-trapping	*2.1 (1.8)	*18.3 (11.4)
Meadow vole	Snap-trapping	*3.4 (4.2)	*1.0 (1.5)
Prairie vole	Snap-trapping	0.1	0
House mouse	Snap-trapping	5.7 (6.9)	6.3 (9.6)
Thirteen-lined ground squirrel	Live-trapping[b]	1.6 (2.4)	0.6 (0.9)
Franklin's ground squirrel	Live-trapping	0.4 (0.6)	0 (0)
Plains pocket gopher	Mound count[c]	*3.6 (1.7)	*1.8 (1.9)
Eastern cottontail	Bounded count[d]	*0.6 (0.8)	*2.7 (1.8)
	Winter track frequency[e]	*1.2 (1.1)	*2.8 (0.4)
Eastern mole	Percent occurrence[f]	21	50
Raccoon	Percent occurrence	43	67
Weasel spp.	Percent occurrence	14	17
Badger	Percent occurrence	43	0
Striped skunk	Percent occurrence	29	33
Red fox	Percent occurrence	29	50
Woodchuck	Percent occurrence	0	67
Fox squirrel	Percent occurrence[g]	0	67
Whitetailed jackrabbit	Percent occurrence	7	0
White-tailed deer	Percent occurrence	50	83

[a] Averages of values of 14 herbaceous plots and 6 woody plots. Standard deviations are in parentheses. Asterisks indicate a significant difference (two-tailed Student-t test $P \leq 0.05$).

[b] Values are average numbers trapped per plot.

[c] Values are average numbers of gophers estimated per plot.

[d] Values are overall averages of bounded count estimates over 6 census periods.

[e] Values are averages of following codes: 3--tracks frequent (observed on many days); 2--tracks frequent but uncommon (observed only in a small portion of the plot); 1--tracks infrequent; 0--tracks absent.

[f] Percent of plots species known to have occurred in.

[g] Fox squirrel tracks were also positively correlated ($r \geq 0.55$, $P \leq 0.02$) with the amount of woody vegetation on study plots.

The Upland Sandpiper is one of the rarest grassland nesting birds in Iowa (Roosa 1977a). I found the species on only one study plot, in the vicinity of much pastureland and cropland planted with oats. These birds have relatively large territories (Harrison 1975, Wiens 1969), and their tendency to form loose colonies (Bowen 1975, Harrison 1975) greatly increases the amount of grassland required. Probably the species cannot exist on railroad ROWs alone. In fact, most of the locally scarce birds (Arbib 1978, Claugus 1978, Roosa 1977a) which occurred on the railroad ROWs were not grassland but shrubland species such as the Black-billed Cuckoo, Willow Flycatcher, Warbling Vireo, and Yellow Warbler.

Adjacent land use also affected ROW use by mammals. Deer mice and harvest mice appeared to become concentrated on the ROWs by the plowing of adjacent land, and gopher numbers were larger on ROWs with much adjacent corn (Braband 1979). Locally scarce mammals (Bowles 1975, Roosa 1977b) which utilized ROWs were largely grassland species such as the Franklin's ground squirrel, prairie vole, and white-tailed jackrabbit. In addition, the ROWs were used as apparent travel corridors by at least four mammal species: raccoon, striped skunk, red fox, and white-tailed deer (Braband and Klaas 1981).

TABLE 7. Small mammal species diversity on railroad ROWs in Story County, Iowa, Fall, 1977.

Habitat[a]	N	Shannon Index	Species Richness Index
Herbaceous plots	14	0.559 (0.139)	5.3 (1.2)
Woody plots	6	0.426 (0.196)	4.3 (1.4)

[a] Average values for each index are based on the number of plots (N) in each habitat type. Standard deviations are in parentheses.

CONCLUSIONS

The grasslands on railroad ROWs which I studied were utilized by a variety of bird and mammal species. Railroad ROWs provide habitat which probably helps to maintain the number and diversity of wildlife particularly in intensively agricultural areas. The narrow, strip characteristic of the ROWs appears to be a limitation especially for some bird species. However, it may be a benefit for other species, since the ROWs are accessible over a much greater area than a block of habitat of a similar size would be.

This study was relatively intensive but only surveyed bird and mammal populations for a one-year period. Further studies, especially longer term on the values of railroad grasslands and associated habitats would be desirable. Possible topics to be addressed could include reproductive success. Trautman (1960) found relatively high nesting success of Ring-necked Pheasants on railroad ROWs. Other specific uses by wildlife which could be addressed are the relative use of abandoned and active ROWs and the use of ROWs by badgers or other wide-ranging animals. The impact of wind-borne soil deposition and other perturbations on habitat quality could be investigated. Another important topic would be the use of railroad ROWs compared to other strip habitats especially highway ROWs.

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APPENDIX

Common and scientific names of bird and mammal species referred to in the text and tables.

Birds

American Kestrel (*Falco sparverius*)
Northern Bobwhite (*Colinus virginianus*)
Ring-necked Pheasant (*Phasianus colchicus*)
Upland Sandpiper (*Bartramia longicauda*)
Rock Dove (*Columba livia*)
Mourning Dove (*Zenaida macroura*)
Yellow-billed Cuckoo (*Coccyzus americanus*)
Black-billed Cuckoo (*Coccyzus erythropthalmus*)
Chimney Swift (*Chaetura pelagica*)
Common Flicker (*Colaptes auratus*)
Red-headed Woodpecker (*Melanerpes erythrocephalus*)
Downy Woodpecker (*Picoides pubescens*)
Eastern Kingbird (*Tyrannus tyrannus*)
Willow Flycatcher (*Epidonax traillii*)
Horned Lark (*Eremophila alpestris*)
Tree Swallow (*Tachycineta bicolor*)
Barn Swallow (*Hirundo rustica*)
American Crow (*Corvus brachyrhynchos*)
Black-capped Chickadee (*Parus atricapillus*)
Gray Catbird (*Dumetella carolinensis*)
Brown Thrasher (*Toxostoma rufum*)
American Robin (*Turdus migratorius*)
European Starling (*Sturnus vulgaris*)
Warbling Vireo (*Vireo gilvus*)
Yellow Warbler (*Dendroica petechia*)
Common Yellowthroat (*Geothlypis trichas*)
Northern Cardinal (*Cardinalis cardinalis*)
Indigo Bunting (*Passerina cyanea*)
Dickcissel (*Spiza americana*)
Savannah Sparrow (*Passerculus sandwichensis*)
Grasshopper Sparrow (*Ammodramus savannarum*)
LeConte's Sparrow (*Ammodramus leconteii*)
Vesper Sparrow (*Pooecetes gramineus*)
Dark-eyed Junco (*Junco hyemalis*)
American Tree Sparrow (*Spizella passerina*)
White-crowned Sparrow (*Zonotrichia leucophrys*)
Fox Sparrow (*Passerella iliaca*)
Lincoln's Sparrow (*Melospiza lincolnii*)
Song Sparrow (*Melospiza melodia*)
Snow Bunting (*Plectrophenax nivalis*)
Bobolink (*Dolichonyx oryzivorus*)
Western Meadowlark (*Sturnella neglecta*)
Red-winged Blackbird (*Agelaius phoeniceus*)
Northern Oriole (*Icterus galbula*)
Common Grackle (*Quiscalus quiscula*)
Brown-headed Cowbird (*Molothrus ater*)
American Goldfinch (*Carduelis tristis*)
House Sparrow (*Passer domesticus*)

Mammals

Eastern mole (*Scalopus aquaticus*)
Short-tailed shrew (*Blarina brevicauda*)
Masked shrew (*Sorex cinereus*)
Raccoon (*Procyon loter*)
Weasel (*Mustela* spp.) Striped skunk (*Mephitis mephitis*)
Badger (*Taxidea taxus*)
Red fox (*Vulpes fulva*)
Woodchuck (*Marmota monax*)
Franklin's ground squirrel (*Spermophilus franklini*)
Thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*)
Fox squirrel (*Sciurus niger*)
Plains pocket gopher (*Geomys bursarius*)
House mouse (*Mus musculus*)
White-footed mouse (*Peromyscus leucopus*)
Deer mouse (*Peromyscus maniculatus*)
Western harvest mouse (*Reithrodontomys megalotis*)
Meadow vole (*Microtus pennsylvanicus*)
Prairie vole (*Microtus ochrogaster*)
White-tailed jackrabbit (*Lepus townsendi*)
Eastern cottontail rabbit (*Sylvilagus floridanus*)
White-tailed deer (*Odocoileus virgianus*)

BIRDS WINTERING ON THE KONZA PRAIRIE RESEARCH NATURAL AREA

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Abstract. Wintering birds were censused along 16 permanent transects (13 in prairie and three in gallery forest) that were established within the Konza Prairie Research Natural Area (KPRNA) 10 km south of Manhattan, Kansas. Each transect was censused once in the first two weeks of January during 1982-1984. The prairie transects were either burned or unburned the previous spring and ungrazed by large herbivores for at least six years. Significantly more individuals per km and more species were observed in the gallery forest than in the prairie. The red-headed woodpecker (*Melanerpes erythrocephalus*) was the most abundant species during 1982 and 1984 in the gallery forest, while black-capped chickadee (*Parus atricapillus*) was the most abundant in 1983. The abundance of red-headed woodpecker was negatively correlated with the abundance of red-bellied woodpecker (*Melanerpes carolinus*), but not correlated with blue jay (*Cyanocitta cristata*) abundance. Red-bellied woodpecker abundance was not correlated with blue jay abundance. American tree sparrow (*Spizella arborea*) was the most abundant species in the prairie during all three winters.

INTRODUCTION

Winters in the Northern Great Plains are harsh and variable both within a season and from year to year. Fretwell (1972) suggested that winter may be the time of year when most temperate-zone bird populations are regulated. However, few studies on wintering birds have been conducted in the tallgrass prairie region of the United States (Grzybowski 1982). Factors that affect bird populations in winter include: space use (Grzybowski 1983a), social organization (Grzybowski 1983b), climate (Kricher 1975, Grubb 1977, Graber and Graber 1979, 1983), resource abundance and competition (Pulliam and Enders 1971, Pulliam and Parker 1979, Dunning and Brown 1982, Grzybowski 1982), and avoidance of predation (Pulliam and Mills 1977). The purpose of this paper is to summarize data on the birds that winter on the Konza Prairie Research Natural Area (KPRNA) in both the prairie and associated gallery forest.

STUDY AREA

The Konza Prairie Research Natural Area, 3,486 ha of tallgrass prairie and associated gallery forest, is located in the Flint Hills 10 km south of Manhattan, Kansas. The prairie is dominated by big bluestem (*Andropogon gerardii*), little bluestem (*A. scoparius*), switchgrass (*Panicum virgatum*), and indian grass (*Sorghastrum nutans*) (Freeman and Hulbert 1985). Six percent of KPRNA is gallery forest dominated by bur oak (*Quercus macrocarpa*), chinquapin oak (*Q. muehlenbergii*) and hackberry (*Celtis occidentalis*) (Killingbeck 1984). KPRNA is owned by The Nature Conservancy and managed by Kansas State University for long-term ecological research (LTER). The current management plan on KPRNA includes unburned watersheds and watersheds burned during spring at the following interfire intervals: 1, 2, 4, and 10 years, burned for 3 years then left unburned for 3 years, and finally, those watersheds burned only after wet years, i.e., precipitation of more than 1.2 times the median (Hulbert 1985). Native grazers, bison (*Bison bison*), antelope (*Antilocapra americana*), and elk (*Cervus elaphus*), may be added in the future. The areas used in this study have never been plowed and have not been grazed by cattle since at least 1976.

Winters on KPRNA area are quite variable. The area is just below the permanent winter snow belt. During the three years of this study mean maximum temperature for Manhattan during January was 0.9, 3.8, and 2.7° C for 1982, 1983, and 1984, respectively, while mean minimum temperature was -11.2, -5.1, and -8.5° C, and January precipitation was 28.7, 31.0 and 7.6 mm (Weather Data Library, Kansas State University).

METHODS

Wintering birds were censused on 13 transects (total length = 9.9 km) in the prairie and three transects (total length = 2.9 km) in the gallery forest. The transects, ranging in length from 0.38 to 1.49 km, were permanently established to monitor the bird populations for LTER on KPRNA. Each transect was censused one time per year during the first two weeks of January 1982-1984. The censuses were started within 3 hrs of sunrise on days when the wind speed was less than 4.5 m/sec, temperature was greater than - 28.9° C and there was no heavy rain or snow. The transects, censused in a random order, were walked at a rate of 1.3 km per hour. For each observation, species, sex, and perpendicular distance from the transect line were recorded.

Chi-square analysis was used to test for differential, or nonrandom, use of prairie versus gallery forest. The number of birds expected in a treatment was calculated from the proportion of the total distance of census lines in that treatment multiplied by the total number of birds seen on all censuses. Pearson product-moment correlation was used to test for relationships among the species in the gallery forest that rely heavily on mast crop, i.e., red-headed woodpecker, red-bellied woodpecker, and blue jay (see Appendix 1 for scientific names).

RESULTS AND DISCUSSION

Thirty species of birds were observed in the gallery forest; nine of which (30%) were observed all three years (Table 1). The red-headed woodpecker was the most abundant species in 1982 and 1984, while the black-capped chickadee was the most abundant in 1983. Together these two species accounted for an average of 41% of the observations over the three year period (Table 1). Red-headed woodpecker abundance was positively related to the magnitude of mast crop in Illinois (Williams and Batzli 1979). A negative correlation between red-headed woodpecker density and red-bellied woodpecker density in the three gallery forest areas over the three years ($r = -0.735$, d.f. = 7, $p < 0.05$) was observed on KPRNA. Interspecific territoriality and aggression have been shown between these two species (Moskovits 1978, Williams and Batzli 1979). No significant correlation between number of blue jay and red-headed woodpecker ($r = 0.607$, d.f. = 7, $p > 0.05$), nor between number of blue jay and red-bellied woodpecker ($r = -0.660$, d.f. = 7, $p > 0.05$) existed. These mast eating species accounted for 32.8, 19.1, and 61.4% of the observations in 1982, 1983, and 1984, respectively. Availability of food is probably the underlying cause behind the yearly changes in numbers of these three species on KPRNA with 1.15, 0.44, and 0.23 g/0.25 m^2 of seeds in the gallery forest for 1981, 1982, and 1983, respectively (Seastedt, unpubl. data). Estimates of mast crop are unavailable, but subsequent analysis indicates that 80-90% of the seed biomass produced in the KPRNA gallery forest are acorns (Briggs, personal communication).

Black-capped chickadee, white-breasted nuthatch, and blue jay were the second most abundant species in 1982, 1983, and 1984,

respectively. White-breasted nuthatch is a member of the North American bark-foraging guild during the winter (Grubb 1982). The black-capped chickadee is frequently found in small flocks (4-8 members) during the winter (Ficken 1981). The blue jay responds to mast crop and is an important dispersal agent for acorns (*Quercus* spp.) (Darley-Hill and Johnson 1981).

Twenty species were observed in the gallery forest in 1982, while 21 and 15 species were observed in 1983 and 1984, respectively. In comparison Emlen (1972) observed 35 species in a south Texas river forest in one year. The average of 18.7 species observed in the gallery forest is lower than the 22 species found in a New Jersey oak forest by Kricher (1975) during a two year study and the 37 species in bottomland forests and 30 species in upland forests in Illinois (Graber and Graber 1979). While partial explanation of these differences may be due to differences in methodology, size of the woodland tract, and latitude effects are also possible causes for the differences. For example, Drennan (1981), using the Christmas Bird Count data, has demonstrated increased number of species as one goes south. On average 21% of the species wintering in the gallery forest on KPRNA are winter residents (see Appendix 1 for seasonal status), which is lower than the 51% in a south Texas river forest (Emlen 1972).

Twenty-four species of birds were observed in the prairie over the three years; four of which (16.7%) were observed all three years (Table 2). The American tree sparrow, ranging from 28.3 to 78.7% of the individuals observed, was the most abundant species all three years. Finzel (1964) found horned lark the most abundant wintering species in herbaceous communities of southeastern Wyoming. Grzybowski (1982), studying grasslands with varying grazing intensities, found the most abundant species during the winter to be: Smith's longspur in northern Oklahoma; American tree sparrow, savannah sparrow, Le Conte's sparrow, Smith's longspur, cheshnut-collared longspur or eastern meadowlark in central Oklahoma; horned lark or western meadowlark in western Texas; and savannah sparrow, Le Conte's sparrow, eastern meadowlark or Sprague's pipit in southern Texas.

Many grassland wintering birds are habitat specialists (Grzybowski 1976) and these habitat types are not present in ungrazed tallgrass prairie. The American tree sparrow, the most abundant species on KPRNA in the prairie, is more typical of non-grassland habitat (Bent 1968). In Oklahoma on a moderately grazed site where bird densities were low, Grzybowski (1982) found the American tree sparrow the most abundant species for one of two years and even then the density of American tree sparrow was low. Of the grassland species that typically winter in northeast Kansas, the horned lark and Smith's longspur are usually in heavily grazed areas (Grzybowski 1982). These species are occasionally observed on KPRNA in disturbed areas along trails (Zimmerman, personal communication, personal observation). Lapland longspur prefers cultivated fields (Grzybowski 1982) and are rarely observed on KPRNA (Zimmerman, personal communication). As grazing intensifies with the addition of the large native herbivores, winter use of KPRNA by horned lark and Smith's longspur should increase.

Northern harrier, northern flicker, and black-capped chickadee were the second most abundant species in the prairie during 1982,

TABLE 1. Relative frequency (%) of birds wintering in the gallery forest Konza Prairie Research Natural Area.

Species	Year 1982	1983	1984	Mean
Red-headed woodpecker	27.1	12.1	40.9	26.8
Black-capped chickadee	20.0	15.8	6.8	14.2
Blue jay	4.3	1.7	18.2	8.2
White-breasted nuthatch	2.1	14.0	5.7	7.3
Downy woodpecker	3.6	5.3	3.4	4.1
Northern cardinal	9.3	-	2.3	3.9
Northern bobwhite	-	10.5	-	3.5
Red-bellied woodpecker	1.4	5.3	2.3	3.0
American tree sparrow	4.3	0.9	3.4	2.9
Dark-eyed junco	6.4	1.7	-	2.7
American robin	2.9	1.7	2.3	2.3
Purple finch	-	-	6.8	2.3
Golden-crowned kinglet	2.1	3.5	1.1	2.2
American crow	-	4.4	2.3	2.2
Mallard	6.4	-	-	2.1
Tufted titmouse	2.9	6.1	-	2.0
American goldfinch	-	5.3	-	1.8
Red-tailed hawk	1.4	2.6	-	1.3
Northern flicker	-	1.7	2.3	1.3
Eastern bluebird	2.1	-	1.1	1.1
Brown creeper	-	2.6	-	0.9
Hairy woodpecker	0.7	-	1.1	0.6
Belted kingfisher	-	1.7	-	0.6
Harris' sparrow	-	0.9	-	0.3
Ring-necked pheasant	-	0.9	-	0.3
European starling	-	0.9	-	0.3
Rufous-sided towhee	0.7	-	-	0.2
Northern harrier	0.7	-	-	0.2
Great horned owl	0.7	-	-	0.2
Lincoln's sparrow	0.7	-	-	0.2
Total number of individuals	140	114	88	

Total length of transect in gallery forest = 2.924 km

TABLE 2. Relative frequency (%) of birds wintering in the prairie on Konza Prairie Research Natural Area.

Species	Year 1982	1983	1984	Mean
American tree sparrow	78.7	27.3	28.2	44.7
Black-capped chickadee	1.3	9.1	22.5	11.0
Northern flicker	0.4	21.2	4.2	8.6
Northern harrier	4.9	6.1	2.1	4.4
Pine siskin	-	-	12.7	4.2
European starling	-	-	11.3	3.8
American goldfinch	-	3.0	7.0	3.3
Eastern meadowlark	1.8	6.1	-	2.6
Greater prairie-chicken	2.7	3.0	-	1.9
Great horned owl	-	3.0	2.8	1.9
Downy woodpecker	0.4	3.0	1.4	1.6
Dark-eyed junco	1.8	-	2.8	1.5
Song sparrow	0.4	3.0	-	1.1
Lincoln's sparrow	-	3.0	-	1.0
American crow	-	3.0	-	1.0
Loggerhead shrike	-	3.0	-	1.0
American robin	-	1.4	-	0.8
Red-headed woodpecker	-	1.4	-	0.8
Red-bellied woodpecker	1.3	-	-	0.4
American kestrel	0.9	-	-	0.3
Ring-necked pheasant	0.4	-	-	0.1
Blue jay	0.4	-	-	0.1
Rough-legged hawk	0.4	-	-	0.1
Red-winged blackbird	0.4	-	-	0.1
Total number of individuals	225	33	71	

Total length of transect in the prairie = 9.906 km

1983, and 1984, respectively (Table 2). The black-capped chickadee is typically considered a woodland species, but can be found on the prairie because of invasion of isolated trees and shrub patches along ravines. Black-capped chickadee also forage on stems of stout forbs such as annual sunflower (*Helianthus annuus*) (personal observation). Fifteen species were observed in the prairie in both 1982 and 1983 with ten in 1984. Grzybowski (1982) observed 23 non-raptorial species in grazed grasslands and cultivated fields in Texas and Oklahoma over a three year period. He found 1-11 species per site with an average of 3.5 species per site. On average 27% of the species wintering in the prairie on KPRNA are winter residents (Appendix 1), which is much lower than 73% in Oklahoma, 67% in western Texas, and 71% in southern Texas (Grzybowski 1982). However, he considered only non-raptorial species in areas selected to be relatively open, i.e., without trees or other woody vegetation (Grzybowski, personal communication). In contrast, the KPRNA data represent all species observed, including raptors and those species in isolated trees or shrub patches on the prairie.

More individuals were observed in the gallery forest than expected from a pattern of random use of habitats (1982: $X^2 = 50.2$, d.f. = 1, $p < 0.01$; 1983: $X^2 = 250.5$, d.f. = 1, $p < 0.01$; 1984: $X^2 = 95.4$, d.f. = 1, $p < 0.01$), while fewer individuals were observed in the prairie (Table 3). The number of individuals per km in the gallery forest ranged from a low of 30.1 in 1984 to a high of 47.9 in 1982, while in the prairie the number of individuals per km ranged from a low of 3.3 in 1983 to a high of 22.7 in 1982. Eight of the 37 species (21.6%) observed during the study were seen only in the prairie, while 14 species (37.8%) were observed only in the gallery forest. Many investigators have shown that number of species and individuals of birds increases with structural diversity of the habitat (e.g., MacArthur and MacArthur 1961). Of the birds seen only in the prairie the greater prairie-chicken, eastern meadowlark, and northern harrier are the only species typically found in grasslands during winter. Apparently, woody vegetation is important to birds wintering on KPRNA, even those observed using the prairie.

In summary, the richness of species assemblages that winter on the prairie proper of KPRNA is very low. Most species observed are more typical of non-grassland areas, especially woody or shrubby habitats. The lack of grazing may account for some of this low diversity, since relatively open areas created by grazing may be required by those species that more typically winter on grasslands (Grzybowski 1983a, 1983b). Also, north-eastern Kansas is just below the permanent snow belt, which may make the assemblage of wintering birds different from those to the north that are adapted to snow cover and those to the south that are more adapted to warmer winters. Seed production by the dominate grasses on KPRNA is highly variable (personal observation) and this variability may not be conducive to stable assemblages and high numbers of wintering birds in ungrazed prairie. Further studies on wintering birds are continuing on KPRNA.

TABLE 3. Comparison between the number of individuals in the gallery forest and the prairie on the Konza Prairie Research Natural Area.

Habitat	Year 1982	1983	1984
Gallery forest	140	114	88
Prairie	225	33	71
TOTAL	365	147	159

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APPENDIX I. Scientific names and seasonal status on Konza Prairie Research Natural Area of birds mentioned in paper. W = winter resident, P = permanent resident, S = summer resident, T = transient, X = not present on KPRNA.

Common Name	Scientific Name	Seasonal Status
Mallard	*Anas platyrhynchos*	W
Northern harrier	*Circus cyaneus*	P
Red-tailed hawk	*Buteo jamaicensis*	P
Rough-legged hawk	*Buteo lagopus*	W
Ring-necked pheasant	*Phasianus colchicus*	P
Greater prairie-chicken	*Tympanuchus cupido*	P
Northern bobwhite	*Colinus virginianus*	P
Great horned owl	*Bubo virginianus*	P
Belted kingfisher	*Ceryle alcyon*	P
Red-headed woodpecker	*Melanerpes erythocephalus*	P
Red-bellied woodpecker	*Melanerpes carolinus*	P
Downy woodpecker	*Picoides pubescens*	P
Hairy woodpecker	*Picoides villosus*	P
Northern flicker	*Colaptes auratus*	P
Horned lark	*Eremophila alpestris*	P
Blue jay	*Cyanocitta cristata*	P
American crow	*Corvus brachyrhynchos*	P
Black-capped chickadee	*Parus atricapillus*	P
Tufted titmouse	*Parus bicolor*	P
White-breasted nuthatch	*Sitta carolinensis*	P
Brown creeper	*Certhia americana*	W
Golden-crowned kinglet	*Regulus satrapa*	W
Eastern bluebird	*Sialia sialis*	P
American robin	*Turdus migratorius*	P
Sprague's pipit	*Anthus spragueii*	T
Loggerhead shrike	*Lanius ludovicianus*	P
European starling	*Sturnus vulgaris*	P
Northern cardinal	*Cardinalis cardinalis*	P
Rufous-sided towhee	*Pipilo erythrophthalmus*	P
American tree sparrow	*Spizella arborea*	W
Le Conte's sparrow	*Ammodramus leconteii*	T
Song sparrow	*Melospiza melodia*	W
Lincoln's sparrow	*Melospiza lincolnii*	T
Harris' sparrow	*Zonotrichia querula*	W
Dark-eyed junco	*Junco hyemalis*	W
Lapland longspur	*Calcarius lapponicus*	W
Smith's longspur	*Calcarius pictus*	T
Chestnut-collared longspur	*Calcarius ornatus*	X
Red-winged blackbird	*Agelaius phoeniceus*	S
Eastern meadowlark	*Sturnella magna*	P
Western meadowlark	*Sturnella neglecta*	P
Purple finch	*Carpodacus purpureus*	W
Pine siskin	*Carduelis pinus*	W
American goldfinch	*Carduelis tristis*	P

SEASONAL PHENOLOGY AND HABITAT SELECTION OF THE SEDGE WREN *CISTOTHORUS PLATENSIS* IN A RESTORED TALLGRASS PRAIRIE

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Abstract. The Sedge Wren *Cistothorus platensis* is a regular and abundant summer resident of restored tallgrass prairie plots on the Knox College Field Station in west-central Illinois. Arrival is correlated with the late but rapid growth of the warm-season grasses with the males arriving during the last week in June when the prairie has reached a height of about 1 meter. Females arrive 2 weeks later. Sedge wrens showed a definite preference for recently burned plots with tall, new growth and a clear, litter-free understory, but were observed entering no-burn plots to gather litter for nest building. Nesting activities occurred from the second week in July to fledging of young in late August and early September. Only one clutch per female was observed. Young and adults continued to forage for insects until mid-October when migration is triggered by several nights of hard frost. Two different seasons and two different sized areas yielded similar density data of 9 males and 3 females occupying 10.2 hectares the first season and 17 males and 7 females occupying 24.4 hectares the second season. For both years it took 3.4 hectares of burned prairie to effectively establish 1 pair of wrens. Territories of paired males were further apart than territories of unmated males. It is suggested that mesic, tallgrass prairie is a highly suitable habitat for this species.

INTRODUCTION

As a part of on-going studies of the vertebrates occurring in a small, restored prairie in west-central Illinois, preliminary data have been collected on the sedge wren (*Cistothorus platensis*), formerly known as the short-billed marsh wren (Kroodsma and Verner 1978), which is a regular summer resident of these man-created, tallgrass prairie habitats. This paper reports preliminary findings on the regular use of this mesic prairie habitat, the seasonal phenology of arrival and departure, territoriality, nesting, fledging, and how such activities are influenced by vegetation height. Colony density, and habitat selection of burned versus non-burned prairie are also reported. Knox College students and staff have been studying the effects of fire, litter reduction and litter accumulation on small mammals and birds in this restored prairie for two decades (Schramm 1970, Springer and Schramm 1972, Krohne et al. 1973, Schramm and Willcutts 1983). This sedge wren study has recently become a part of this continuing effort to understand the influence of fire on the prairie community.

THE STUDY AREA

This study was conducted on the Knox College Biological Field Station located 33 km east of Galesburg, Knox County, Illinois, in a restored tallgrass prairie habitat. The study area consisted of contiguous prairie plots of various ages (five to sixteen years old), dominated by a mixed stand of tall grasses big bluestem (*Andropogon gerardi*) and Indian grass (*Sorghastrum nutans*) of relatively uniform structure. These two species together provided about 80% of the plant structure on the prairie plots. Prairie switch grass (*Panicum virgatum*) formed significant clumps in certain parts of the study area. Prairie forbs were also present and scattered throughout the stands, including tall species such as compass plant (*Siphium laciniatum*) and prairie dock (*S. terebinthinaceum*), which provided prominent perching sites for singing male sedge wrens. Some lower-profile forbs included pale purple coneflower (*Echinacea pallida*), yellow coneflower (*Ratibida pinnata*), stiff goldenrod (*Solidago rigida*), prairie clovers (*Petalostemum* sp.), showy tick trefoil (*Desmodium canadense*), and rattlesnake master (*Eryngium yuccifolium*). Some non-prairie, weedy species such as tall goldenrod (*Solidago altissima*), and sweet clover (*Melilotus* spp.) were also present in varying amounts. The presence of these forbs added diversity to the stands, but the basic structure of these prairie habitats was determined by the grasses, their density and height as influenced by stage of seasonal growth and the occurrence of a pre-season prairie burn.

In all years of the study there were no-burn plots as well as recently burned plots for the sedge wrens to choose from. Burning was conducted in early spring, usually in March, well before the prairie began to grow. No-burn plots had not been burned for one to several years with a resultant accumulation of litter and standing-dead material which formed a dense and cluttered understory from ground level up to 0.5 meters. Burned plots always had much more growth (two to three times greater height and density) of new plant material than no-burn plots, but had a clean and unclutterd understory and almost no litter at ground-level.

MATERIALS AND METHODS

The data for this study were gathered over a period of five summers from 1977 through 1982. Two of these summers (1977 and 1981) were more intensive studies with data collected on densities of unmarked individuals, pairs and territories. Observations during other summers contributed to information on arrival dates, departure dates, burn versus no-burn habitat selection, and other aspects of seasonal activity.

Observations on the sedge wrens were made by walking through the habitat or observing with binoculars from stationary positions and recording data on field maps of the various contiguous prairie plots. Observations were made from after the burning period in April to late October. The most intensive field work was carried on in June and July, during the height of wren activity. Wrens were located by sightings and listening for the songs. Birds were easier to locate early in the season, just after arrival (late June), but became increasingly difficult to observe as the height of the grasses increased. During the latter part of the study, tall step-ladders were used as movable observation platforms. It became obvious early in the study that the wrens were attracted to undisturbed grass habitat that developed considerable height and dense under-structure. Regular movement of observers through the habitat tended to knock down the developing grasses and decrease the very structure that was attracting the birds. Hence, an effort was made to limit, as much as possible, such disturbance. Detailed habitat sweeps were not carried out. Thus, the amount of refined data that could be gathered on numbers of the secretive females and nest sites was limited. There was a trade-off between collecting refined data and having the sedge wrens performing in a relatively undisturbed and natural environment. The above situation, coupled with the fact that these tall grasses get up to 2.5 meters, with a great density of stems and understory resulted in less than ideal conditions for collecting observational data. In spite of this situation, the data on male sedge wrens are thought to be fairly reliable due to vocal advertising and prominence of territorial behaviors. Data on females are probably less reliable but we have used it to make conservative estimates of females present. Many observations of non-singing sedge wrens were made

throughout the study, and our estimates of female numbers are based on these observations.

Immediately after arrival, males commence singing and establishing territories. Initially, a newly established male was located, recorded on field maps and then flushed repeatedly from perch to perch. They usually made a circle, flying from one elevated grass or forb stem to the next, vocalizing repeatedly, thus defining a selected area they seem reluctant to leave. These flush-perch recorded territories were later compared to non-disturbed sightings to determine the final locations and numbers of established males.

Fall observations were recorded on adults and fledged young in rather a unique fashion from a tractor during selective combining for grass seed in some of the prairie plots. The combining operation functioned as a good flushing device for large areas, to determine presence or absence (departure), age ratios and dispersion of the late season colony.

The total area of prairie studied in any one year varied throughout the study. In 1977 the intensively studied area was 10.2 hectares. By 1981 more restored area had matured enough to attract sedge wrens, and the study area was increased to 24.4 hectares.

RESULTS AND DISCUSSION

Arrival

Figure 1 depicts the seasonal phenology of sedge wren arrival, breeding activities, and fall migratory departure plotted against average height of the dominant vegetation (prairie grasses). In this study male sedge wrens never arrived earlier than the last week in June, with the population building through the first week in July. At the time of the first arrivals, big bluestem and Indian grass average just under 1 meter in height. The sudden appearance of sedge wrens is very dramatic. In two to three days the prairie is alive with the buzzing trill and visual prominence of male sedge wrens establishing their territories. By July 10th the male population is well established and a few females may also be observed. Females do not sing, are more secretive and harder to observe. They generally showed up about 2 weeks later than the earliest arriving males.

Arrival dates are quite variable in other habitats and other parts of the breeding range of this species. This species has been characterized as opportunistic in its occurrence and timing of breeding efforts (Burns 1982, Meanley 1952, Sherman 1952, Kroodsma and Verner 1978). In sedge meadows, in the more northern parts of its range, it may arrive and breed much earlier from early May to early June (Mousley 1934, Walkinshaw 1935, Crawford 1977, Burns 1982) quite possibly due to the earlier growth of these cool-season species. In late developing rice fields of Arkansas, arrival and breeding activities did not get underway until mid July when the rice plants and associated weeds were approaching a height of 1 meter (Meanley 1952). In this late developing phenology, males were still singing and a nest contained young as late as September 10. In the burned prairie habitats of our study, arrival was extremely predictable. The study plots went from a no-cover, freshly burned area to a well structured, lush habitat resulting from the late starting but rapidly developing growth of the warm-season grasses.

Habitat Selection

The late arrival of sedge wrens, their successful use and obvious attraction to these restored tallgrass prairies is of great interest. An early June bird census would obviously have missed this species. With the demise of the vast areas of mesic grassland from plowing and over-grazing, sedge wren breeding habitat may also have been greatly reduced. The structure of this vegetation, its height and lushness, its abundant insect life and its clean, litter-free, post-fire understory seems to attract this species. Warm-season grasses do

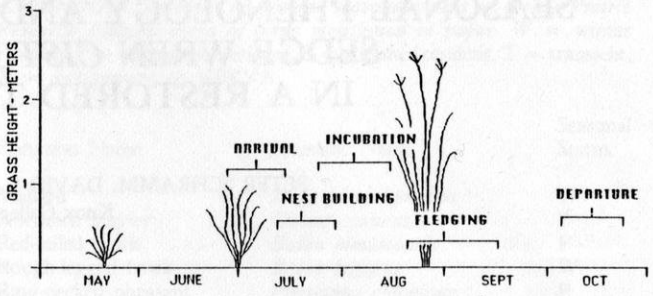

FIG. 1. Seasonal phenology of the sedge wren *Cistothorus platensis* showing arrival, nesting activities, fledging and departure in relation to time and height of the prairie.

not provide enough cover until late June in Illinois. Once the necessary height of about 1 meter has been reached the sedge wrens show up. The clear, post-burn understory is also an important part of their preferred habitat. They are well protected overhead by the new growth and have a clear understory and ground area to move around in and forage for their insect diet. Sedge wrens have been observed in a variety of herbaceous community types but invariably they consist of lush, mesic to damp habitats with good herbaceous structure (Bent 1948, Mousley 1934, Walkinshaw 1935, Meanley 1952, Crawford 1977, Burns 1982). Such habitats must be undisturbed for the most part, or only lightly grazed if they are to attract sedge wrens. Skinner (1975) found a direct correlation of grass height with sedge wren numbers, as affected by grazing, with highest numbers observed in idle fields.

Sedge wrens have been observed by the authors in two other prairie habitats beside the Knox Field Station. S. Johnson observed a singing male seemingly well established, in a remnant prairie cemetery of 0.25 hectares in Bureau County, Illinois. P. Schramm observed the timing of occupancy of a newly established stand of 50/50 big bluestem and Indian grass recently in a privately owned field of 3.6 hectares in Knox County, Illinois. This particular field was planted with grass seed in late spring, went through 2 growing seasons with no wrens, then had its first good burn the third spring and had sedge wrens establish and successfully breed the third growing season.

These observations suggest that this species was probably a summer breeding resident in the original prairies of Illinois at the time of and prior to settlement. Since most of the eastern and mesic portions of the original tallgrass prairie have been destroyed, and undisturbed grasslands and sedge meadows are becoming increasingly rare, today this species is observed primarily in undisturbed herbaceous cover of wetland edges. When it is presented with an ungrazed plot of restored, warm-season, native grasses, in a high rainfall region such as Illinois, it will occupy this lush habitat by the third growing season. With continued expansion of prairie restoration efforts in these high-rainfall areas, it can be predicted that sedge wren populations will flourish in these new prairie habitats.

Use of Burned Plots

It became apparent early in the study that the wrens were attracted to the most recently burned prairie plots. In accordance with field station management plans certain areas were left unburned each year, to provide comparative study areas for several on-going animal studies. The sedge wrens, like other prairie animals had their preferences. Figure 2 depicts territories and areas of high activity in relation to burn plots (burned the spring before arrival) and no-burn plots. The territories shown are newly established areas selected soon after arrival. The total area of burned prairie shown in this figure and available to the wrens in 1977 was 10.2

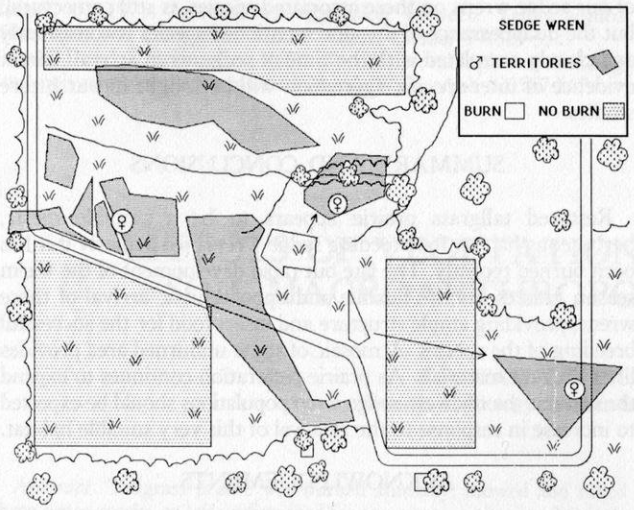

FIG. 2. Map of the burned and unburned prairie study area of 1977 showing territory shifts and dispersion of paired and unpaired sedge wren males.

hectares. Wrens appear to use recently burned areas almost exclusively, when such are available. They rarely enter no-burn areas except during nest building when they may frequent such areas to gather dry litter and dead grass leaves for their characteristic domed and woven nests. Such materials are non-existent in the burned habitats. This points up the need for some mosaic of burned and unburned habitat to supply the complete needs of this species. The burned plots always resulted in much higher (2.5 times greater height) and denser above-ground structure than the unburned plots, and at the same time, provided a clear, litter-free understory foraging area, hidden deep within the developing prairie structure. Such clear understory not only provides foraging area but also escape space for the secretive females and newly fledged young.

Nesting Activities

Nest building was observed during the latter 3 weeks of July (Fig. 1) when both sexes collected nest materials. This is the time when wrens may be seen entering no-burn plots to collect dead grass material. Nests are very hard to find in this tall, dense habitat without a detailed and disruptive search effort. Since non-disturbance to the habitat structure was of primary concern, nest searching sweeps were not undertaken, hence nest data are meager. Six active nests, woven into dense grass clumps from 0.8 to 1 meter above the ground, were found. This height is somewhat greater than reported in other studies (Mousley 1934, Walkinshaw 1935, Meanley 1952), but may be related to the higher profile of mesic tallgrass prairie vegetation. All the nests found were in actual use. Dummy nests have been reported for this species (Mousley 1934, Walkinshaw 1935, Burns 1982) and may play a role in pair formation (Verner 1964, Verner and Engelson 1970). None were documented during this study, but may have been present in the dense habitat, and simply not found.

With the initial late arrival, there seems to be only enough time for the production of one clutch, and observations seem to support this conclusion. This does not, however, rule out renesting after nest destruction by a predator.

Incubation and care of young in the nest occurs from late July to late August. Wrens were observed carrying insect food to the few nests observed at this time. Other studies report a rather consistant 14 day incubation period and a 11 to 16 day fledging age (Mousley 1934, Walkinshaw 1935, Crawford 1977, Burns 1982). This agrees with the phenology of nesting activities observed in this study.

Adult male singing and visual perch display is greatly reduced by August, has completely ceased by September, and the sexes are behaviorally indistinguishable.

The first fledged young were sighted or flushed from the last week of August to mid September. The young are more secretive than the adults but can be found by surprise flushing from the deep grass. They are weak fliers that struggle up out of the grass, fly for only a few meters and then literally fall or tumble back into the dense vegetation and flutter to ground level. Like Walkinshaw (1935), we observed sedge wrens moving close to ground level like mice. The clear understory of the burned plots may provide an easier microhabitat for these young birds to move around in. Upon flushing, adults can be distinguished from the young by their stronger wingbeat and further flight (10 or more meters) before they too "fall" in characteristic fashion back into the prairie. Such weak flying young were flushed with regularity, throughout September. Seed combining operations in some of the plots, provided an effective flushing procedure, and indicated that by late September and October these fledglings are rather evenly dispersed throughout the burn plots along with adult birds.

The combining operation harvests only the tops of the tall grasses, leaving good cover for the wrens. Flushing observations indicate that the wrens continued to use and forage in the combined plots for the remainder of their stay, even though the vegetation height had been reduced to 1.4 meters. Meanley (1952) reported sedge wren numbers reduced but still persisting after combining of a rice field in Arkansas. Our densities were not reduced by combining.

Departure

Departure occurs after two or three days of hard frost in mid to late October. A night or two of light frost with following warm days is not enough to drive the population southward. There are many insects still active in the prairie at this time, providing food for this insectivorous species. Hard frost and cold days suppress this food source and seem to trigger the sudden exodus of the entire population. Departure can be compared to arrival. When it occurs, it is sudden and dramatic.

Densities and Territoriality

Table 1 shows the densities of wrens for 1977 and 1981, years when good observations and reliable estimates of wren numbers were obtained. That first summer the area of burned prairie was 10.2 hectares in size and had a total number of 12 wrens, 9 males and 3 females. From our observations it appears that the 3 females took up with 3 of the males in rather well spaced out territories (Fig. 2). Two of these territories, that contained females, went through a position shift shortly after establishment (see arrows in Fig. 2), and were spaced out the maximum distance the preferred

TABLE 1. Sedge Wren densities of males, females, and established pairs for two different years.

		Total Number			Densities per Hectare		
Year	Study Area Size	Males	Females	Pairs	Males	Females	Pairs
1977	10.2 Hectares	9.0	3.0	3.0	0.88	0.29	0.29
1981	24.4 Hectares	17.0	7.0	7.0	0.70	0.29	0.29
				Averages	0.79	0.29	0.29

habitat would allow. The 6 remaining unmated males seem to be more tolerant of crowding and had adjoining territories of varying sizes, crowded into the remaining portion of the burned plots. The territories shown were determined shortly after arrival and may well have changed in size and position (particularly those of the unpaired males) as the season progressed. The rapid growth of the prairie at this stage, made it increasingly difficult to keep track of sedge wren positions and numbers.

By 1981, the study area had expanded to over twice the size of the first summer and contained 24.4 hectares of burned prairie, which attracted 24 sedge wrens, 17 males and 7 females. Sedge wren densities for the two different summers and the two different sized areas were quite similar: 0.88 and 0.70 per hectare, respectively, for established males and 0.29 per hectare (identical for both years) for established pairs. For both years it took about 3.4 hectares of burned prairie present to effectively establish 1 breeding pair of sedge wrens. Thirty-three percent of the established males paired with females in 1977 and 41% were paired in 1981. These figures for the second year are considered conservative ones because of the larger study area and the increased quality, density, and maturity of restored prairie. Some additional females may have been present and missed late in the breeding period.

Verner and Willson (1969) suspected polygyny in this species, and Crawford (1977) reported definite evidence of this phenomenon occasionally occurring in the sedge wren. The present study saw no more than one female associated with any one male at one time, but we cannot be sure that there was no polygyny. An excess of males seems to be the rule in the colony structure of this species, with an average ratio of 2.6 males per 1 female, for two years of this study.

ASSOCIATED SPECIES

In the early years of bird observations in the Knox College restored prairies, it was surprising to find a relatively low species diversity. Several edge species were quite evident around the perimeter of the prairie, including yellowthroats (*Geothlypis trichas*), indigo buntings (*Passerina cyanea*), field sparrows (*Spizella pusilla*), and song sparrows (*Melospiza melodia*), but the only other species that moved right out into the prairie and nested in it was the redwing blackbird (*Agelaius phoenioeus*). Like the sedge wren, it too experiences a late arrival (first part of June), nesting about 1 month later in the prairie than it does in local roadside and marsh habitats of this same area. Other species one might expect, such as the bobolink (*Dolichonyx oryzivorus*), dickcissel (*Spiza americana*), and meadowlark (*Sturnella magna*) have shown up in May and early June, appeared to be establishing territories only to move out about the time the wrens arrive in full force. It was well established by our observations that these three species did not nest in the area at an earlier date, and were totally absent by late June.

Two possibilities are presently being considered to explain the absence of these prairie species. The rapid growth and very high profile of these tall grasses in this high rainfall area may be less suitable to these three species than other types of cover in western Illinois. Meadowlarks and dickcissels are common in alfalfa fields and lightly grazed cool-season pastures in this area. Bobolinks are much rarer and found only in very large, unmowed and very lightly grazed cool-season pastures. These habitats are one-third the height of our restored prairie. Another possibility is that the wren's aggressive and prominent "take-over" of these prairies in late June may have a precluding influence on the establishment of these species. Picman and Picman (1980) demonstrated experimentally that both male and female sedge wrens attack (peck) and destroy the eggs of several small passerine species. Other studies have documented a trend in the wren family (Troglodytidae) of aggression toward the nests of competing and sympatrically nesting species (Orians and Willson 1964, Verner 1975, Picman 1977, Kendeigh 1941, Anderson and Anderson 1973). The actual effect of our sedge wrens on these associated species, is still conjectural, but the disappearance of the aforementioned species is consistantly and closely correlated with the time of sedge wren arrival. Direct evidence of inter-specific aggression will be sought in our future studies.

SUMMARY AND CONCLUSIONS

Restored tallgrass prairie appears to be a suitable mesic, herbaceous habitat for breeding sedge wrens, particularly if it has been burned recently. The late but rapid development of the warm season grasses fits the flexible and opportunistic arrival of these wrens, providing ample structure and insect food for the successful breeding of the species. A mosaic of some unburned area provides litter for nest materials. As prairie restoration continues to expand throughout the midwest, sedge wren populations should be expected to increase in response to the renewal of this very suitable habitat.

ACKNOWLEDGEMENTS

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EFFECTS OF VEGETATION, BURNING AND MOWING ON SOIL MACROARTHROPODS OF TALLGRASS PRAIRIE

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Abstract. Tallgrass prairie was burned annually, mowed and raked three times yearly, or left undisturbed for two years, and soil arthropods were censused after the first and second years of treatment. Total arthropod densities increased from about 75 individuals/m² to 132 individuals/m² and arthropod biomass increased from about 24 kg/ha to 43 kg/ha from Nov. 1981 to March 1983. These increases were associated with increased productivity of prairie vegetation during the initial year of the study. Annual burning resulted in increased biomass of root xylem feeders (cicada nymphs); mowing and raking resulted in increased biomass of root chewing insects (white grubs). Smaller herbivores (mostly chrysomelid larvae), predaceous beetle larvae and insect detritivores were most abundant on unburned plots. Overall, arthropod biomass was highest on burned plots; however, densities of arthropods were not significantly different among treatments. Of the arthropods found to be abundant in tallgrass prairie soil, only the white grubs are known to adversely affect plant productivity. Results from this study suggest that drought or land use practices that stress the vegetation will increase densities of these pest insects.

INTRODUCTION

Knowledge of the abundance and trophic composition of the litter and soil inhabiting arthropods of tallgrass prairie is limited. Even less is known about the positive and negative impacts that this group have on the productivity of the prairie, or how various range management practices such as burning, haying or grazing affect the activities of this soil fauna. Best known of the soil arthropods are the root feeders, particularly the larvae of June beetles or white grubs (Hayes 1925, Hayes and McColloch 1928). These insect larvae can cause serious damage to plants and are periodically abundant in most North American grasslands (e.g., Fluke et al. 1932, Ueckert 1979, Wiener and Capinera 1980). A second group of soil herbivores, the cicada nymphs, feed on root xylem fluids and are also abundant in tallgrass prairie (Beamer 1928). No accounts of damage to grassland vegetation have been attributed to this latter group, although damage to tree species has been reported for forest dwelling cicadas (e.g., Karban 1982). Most of the June beetles have life cycles of two or three years (Hayes 1925, Ritcher 1966), while prairie cicada nymphs have life cycles of two to four years (Beamer 1928). Development time of these insects may be influenced by food quality (e.g., Ritcher 1966, Mattson 1980); therefore, land use practices that directly or indirectly affect the quantity and quality of roots and rhizomes could affect survivorship, densities and biomass of the soil herbivores.

In a previous study Seastedt (1984a) reported that biomass of white grubs was higher on tallgrass prairie sites that had been annually burned for four consecutive years compared to measurements obtained from prairie that had not been burned for at least that length of time. Root biomass and productivity on ungrazed grasslands are generally greater on burned prairie sites (Hadley and Kieckhefer 1963, Kucera and Dahlman 1968); however, soil microclimate is also affected by burning (e.g., Weaver and Rowland 1952, Hulbert 1969). Thus, a causal relationship between plant productivity and densities of these soil herbivores could not be established. The present study employed an experimental approach to further elucidate relationships between soil arthropod densities and biomass and vegetation characteristics. Prairie not burned for several years was (1) burned annually for two years, (2) mowed and raked three times over the growing season for two years, or (3) left unburned and unmowed. Density and biomass estimates of soil arthropods were related to vegetation changes occurring during the study period and to treatment-induced changes in belowground plant productivity and nitrogen content of living and dead rhizomes and roots.

STUDY SITE AND METHODS

The study was conducted on the Konza Prairie Research Natural Area located about 15 km south of Manhattan, Kansas. Vegetation of this area is typical for tallgrass prairie and was dominated by big bluestem (*Andropogon gerardii* Vitman), Indiangrass (*Sorghastrum nutans* (L) Nash) and switchgrass (*Panicum virgatum* L.). Further details of vegetation composition are reported in Bragg and Hulbert (1976) and Hulbert (1969). The site used in this study was a bottomland area on a watershed that had not been burned for three years. No grazing by cattle had occurred on this site for 10 years. Soils were fine mixed mesic pachic argiustolls formed in colluvial and alluvial sediments, and have been described in Jantz et al. (1975).

A series of 18, 10 m x 10 m plots was established parallel to a stream-bank. Treatments (unburned, burned, mowed and raked three times during the growing season) were blocked to remove the variants that might be due to slope effects. The study was initiated in the spring of 1981, and treatments were continued for two years. Soil arthropods were censused by excavating and hand-sorting two or three 0.1 m² by 20 cm deep soil monoliths per plot (Seastedt 1984a). Rhizomes of grasses were concurrently harvested from these samples and sorted into living and dead components. Arthropods were returned to the laboratory, identified, dried at 70° C and weighed. Samples were obtained when the arthropods were inactive during November 1981 and again in late March and early April of 1983.

Arthropods were identified to family and grouped according to trophic status. Only larger arthropods (macroarthropods) are reported here. Ants and termites were not included in the counts, nor were densities of the very small arthropods (microarthropods). All white grubs (Scarabaeidae) were classified as herbivores; few adult detritivores of this family have been found of ungrazed prairie (Seastedt 1984a).

Most arthropod groups censused in this study exhibited clumped distributions. Therefore, a logarithmic transformation ($y = \log(x + 1)$) was performed prior to statistical analysis to normalize distributions and homogenize variances. Differences in densities

TABLE 1. Growing season (1 April - 30 Sept.) rainfall, temperature and aboveground plant amounts of unburned tallgrass prairie.[1]

	Year		
	1980	1981	1982
Rainfall (mm)	321.0	649.0	623.0
Average temperature (°C)	21.2	21.6	20.8
Vegetation (kg/ha)	2314.0	7423.0	5457.0

[1]Climatic records for Manhattan, Kan. (L.D. Bark, unpublished). Vegetation data are from autumn clippings of the Aldous Plots, located about 15 km from the present study site (C.E. Owensby, unpublished).

and biomass of arthropods attributed to sampling date were assessed by using a two-way ANOVA (date, treatment and interaction) using type-IV sums of squares to establish the potential significance of sampling date. Treatment effects on arthropod densities and biomass were evaluated for each collection date using a one-way ANOVA.

Kucera and Dahlman (1968) established a positive correlation between rhizome and root mass and productivity. Living and dead rhizome mass were therefore used as indices of belowground plant biomass and plant productivity on the treatments. Big bluestem and Indiangrass dominated total rhizome biomass, and only these two species were used in our index of belowground plant productivity. Other indices of plant productivity and nitrogen content of belowground plant materials were obtained from other studies being conducted on Konza Prairie or nearby areas by other investigators.

RESULTS AND DISCUSSION

Arthropod Responses to Changes in the Prairie Environment

Aboveground (and, presumably, belowground) plant productivity of tallgrass prairie was strongly influenced by the temperature and moisture regimes (Table 1). A severe drought in 1980 was followed by two years of above-normal rainfall in 1981 and 1982. Rainfall amounts resulted in low plant productivity in 1980, high productivity in 1981, and moderate productivity in 1982 (Table 1). The vegetation response to the rainfall was believed to have strongly influenced soil arthropod densities and biomass. The biomass produced by the large increase in plant productivity in 1981 initially became available to plant and detritus feeders during the summer of 1981. Increased survivorship of arthropods may

TABLE 2. Soil arthropod densities (number/m²) on unburned, burned and mowed plots of tallgrass prairie.[1]

	TREATMENT							
	1981				1983			
ARTHROPOD GROUP	Unburned (n=18)	Burned (n=15	Mowed (n=8)	All Plots (n=41)	Unburned (n=15)	Burned (n=15)	Mowed (n=15)	All Plots (n=45)
Herbivores (total)	36.7	26.7	28.8	31.4	42.7	50.6	38.7	44.0*
White Grubs	7.2	11.3	8.8	8.8	5.3B	10.0AB	17.9A	11.1
Cicadas	11.1	10.0	13.8	11.2	14.0AB	28.7A	8.0B	16.9
Misc. Insects	18.4	5.4	6.2	9.9	23.4A	11.9B	12.8B	17.0
Predators (total)	2.8	2.6	5.0	3.2	50.7A	13.3B	14.0B	26.0*
Centipedes	1.1	0.6	1.3	0.9	10.7A	0.7B	2.7B	4.7
Predaceous Insects	1.7	2.0	3.7	2.3	40.0A	12.7B	11.3B	21.3*
Detritivores (total)	11.6	26.7	6.3	16.1	60.7	81.3	44.7	62.2*
Millipedes	10.5	26.7	6.3	15.6	49.3	80.0	40.7	56.7*
Misc. Insects	1.0	0.0	0.0	0.4	11.4A	1.3B	4.0AB	5.5
Total	51.1	56.0	40.1	50.7	154.0	145.3	97.3	132.2*

[1]Significant differences between sampling dates or among treatments within a sampling date are indicated by symbols. Means followed by an asterisk (*) indicate higher values for that sampling date ($p < .05$). Means followed by different letters indicate that treatment means were significantly different for that sampling date (Duncan's multiple range test, $p < .05$).

TABLE 3. Soil arthropod biomass (kg/ha) on unburned, burned and mowed plots of tallgrass prairie.[1]

	TREATMENT							
	1981				1983			
ARTHROPOD GROUP	Unburned (n=18)	Burned (n=15)	Mowed (n=8)	All Plots (n=41)	Unburned (n=15)	Burned (n=15)	Mowed (n=15)	All Plots (n=45)
Herbivores (total)	17.1	17.0	19.0	17.4	17.0	30.5	30.3	26.0
White Grubs	9.3	11.7	7.9	9.9	8.1B	11.4B	22.9A	14.2
Cicadas	7.1	4.5	6.8	6.1	7.5B	18.4A	6.0B	10.6
Misc. Insects	0.7	1.8	4.3	2.4	1.4	0.7	1.4	1.4
Predators (total)	0.5	0.4	1.0	0.6	7.1A	2.3B	2.0B	3.8*
Centipedes	0.0	0.1	0.1	0.1	0.2	0.0	0.1	0.1
Predaceous Insects	0.5	0.3	0.9	0.5	6.9A	2.3B	1.9B	3.7*
Dentrivores (total)	4.0	8.4	6.4	6.1	8.4B	20.6A	11.4AB	13.5*
Millipedes	4.0	8.4	6.4	5.6	7.1B	20.4A	11.0B	12.9*
Misc. Insects	0.0	0.0	0.0	0.0	1.3	0.2	0.4	0.6
Total	21.4	22.7	26.4	24.0	32.5B	53.3A	43.8AB	43.2*

[1]Significant difference between sampling dates or among treatments within dates are indicated as in Table 2.

have occurred during this first year of the study; however, increased reproduction of arthropods resulting from greater availability of food resources would not have been measurable by our sampling procedures until the second year of study. Significant increases in the densities of all trophic groups of arthropods were found in the spring 1983 samples compared to estimates obtained in 1981 (Table 2). Total soil arthropod biomass also increased, with much of this increase attributable to predaceous insects and millipedes (Table 3). A uniform response of all fauna was not observed; herbivore biomass did not significantly increase even though the average biomass of the dominant herbivores, the white grubs and cicadas, changed from 16.0 to 24.8 kg/ha during this interval. Overall, results suggest a positive correlation and lag-time between increased productivity of the prairie grasses and increased densities and biomass of soil arthropods.

Arthropod Responses to Burning and Mowing

Significant differences in the biomass of rhizomes of big bluestem and Indiangrass harvested in the spring of 1983 were observed between burned and mowed plots (Table 4). Annual spring burning has been shown to increase belowground productivity (Kucera and Dahlman 1968), while excessive mowing of the tallgrass prairie during the growing season has been shown to seriously stress the vegetation and reduce productivity (Owensby et al. 1974). Both annual burning and mowing will increase growing season soil temperatures and reduce soil moisture (e.g., Hulbert 1969 and unpubl. data); thus, the major differences between these two treatments were their respective effects on plant productivity and the resulting changes in the amounts of living and dead plant material in the soil.

No significant differences among treatments were observed for arthropod biomass estimates obtained in autumn of 1981 following the first year of treatment, which suggests a lag-time between changes in vegetation characteristics and arthropod abundance. By 1983, however, many differences attributed to treatment were observed. Overall, densities of arthropods obtained in the spring of 1983 were not significantly different among treatments, but arthropod biomass was significantly higher on the burned versus the unburned plots (Tables 2 and 3). These findings are consistent with those previously reported by Seastedt (1984a).

Of particular interest was the different response of the herbivore groups to mowing or burning. Cicada nymphs were significantly more abundant on the burned versus the mowed plots, and biomass estimates of cicadas were significantly higher on the burned plots than on either the mowed or unburned plots. These findings differ from those reported by Seastedt (1984a), but are consistent with the hypothesis that the abundance of this group is strongly influenced by root abundance and the activity of these roots. Beamer (1928) presented details on the life-histories of prairie cicadas. These species build a "cell" in the soil and siphon xylem fluids from roots. Cicadas are sedentary and will move about in the soil only if their food resource disappears. A high density of healthy roots, transfering large quantities of xylem fluids to actively transpiring leaves, would provide an optimal habitat for these insects. Accordingly, cicadas should be more abundant on productive sites such as annually burned prairie. Densities and biomass should be adversely affected by drought conditions or by repeated removal of the canopy during the growing season (i.e., by grazing or mowing). Either condition would result in a decline in the volume of xylem fluids. We suggest that the lack of significant differences in cicada numbers between burned and unburned sites reported by Seastedt (1984a) was due to sampling in the year following the 1980 drought.

In contrast to the cicadas, white grubs exhibited increased biomass on the mowed (stressed) plots. Survivorship of white grubs is reported to be adversely affected by wet soil conditions (Davidson and Roberts 1968), and Konza Prairie soils were likely wetter in 1981 and 1982 compared to 1980. Drier soils on the burned and mowed and raked plots relative to unburned plots therefore could have had a positive effect on grub densities, but the dramatic difference in biomass between the mowed and burned plots suggests that other factors were relatively more important.

White grubs feed by eating their way through the soil. Examination of the gut contents of these larvae reveals a large amount of mineral soil mixed with fragments of plant tissues. In burned sites, more roots per unit area of soil are available to these insects, and annual burning over an extended period of time appears sufficient to increase densities and biomass of these insects (Seastedt 1984a). Results from the present study suggested a trend towards greater biomass of grubs on burned sites, but two years of burning were insufficient to result in increased densities of grubs relative to those observed on unburned plots. Again, a lag-time between plant and herbivore response is suggested. Mowing and raking plots three times over the growing season resulted in increased rhizome mortality. Thus, the absolute amount of food resources for herbivores was probably reduced on mowed plots compared to that of burned plots. The senescing and decaying rhizomes and roots of mowed plots, however, had increased nitrogen content (Table 5). This phenomenon results from respiration and nitrogen immobilization by microbes adhering to these decaying tissues (e.g., Clark and Campion 1976). The effect of mowing, then, would result in a time interval when belowground plant mortality causes increased quality of food resources for the white grubs, which apparently results in increased survivorship and growth. A second interpretation of our results that cannot be addressed by this study is that the stressed plants on the mowed plots failed to produce adequate feeding deterents or secondary plant substances that inhibit grazing (e.g., Hargrove et al. 1984). Regardless of the exact mechanisms, the correlation between plant stress and insect herbivore outbreaks has been documented for many foliage and wood feeders (e.g., White 1974, 1976, Waring and Pitman 1983),

TABLE 4. Rhizome mass of big bluestem and Indiangrass on unburned, burned and mowed plots, spring 1983.[1]

	kg/ha (std. error)		
	Unburned	Burned	Mowed
Live Rhizomes	2350 AB (418)	2722 A (383)	1837 B (331)
Dead Rhizomes	256 A (53)	345 A (75)	287 A (70)
Total	2606 AB (394)	3067 A (367)	2124 B (316)

[1]Means followed by different letters are significantly different (Duncan's multiple range test, $p<.05$, $n = 15$ per treatment).

TABLE 5. Nitrogen content (% of mass) of living and dead roots and rhizomes.[1]

Date of	Rhizomes		Roots	
Collection	Live	Dead	Live	Dead
June	0.74 (.02)	0.77 (.02)	0.59 (.02)	0.99 (.03)
July	0.74 (.01)	0.86 (.03)	0.62 (.02)	1.13 (.03)
August	0.72 (.01)	0.77 (.02)	0.61 (.01)	1.05 (.02)
October	0.97 (.02)	0.89 (.02)	0.79 (.03)	1.13 (.03)

[1]Means of 24 samples collected from burned plots on Konza Prairie during the summer and autumn of 1983. Standard errors are in parentheses.

and our results also suggest a relationship between stressed plants and certain root-feeders.

Treatment effects on other soil arthropods are somewhat more difficult to interpret. Miscellaneous soil herbivores (mostly very small chrysomelid larvae) had statistically higher densities on unburned plots. While numerically abundant, this group composed only a small fraction of the total herbivore biomass, and the factors responsible for their abundance remain unknown. Litter was much more abundant on unburned plots than on either the burned or mowed and raked plots. The presence of this substrate likely explains the relatively greater abundance of miscellaneous insect detritivores (mostly diptera larvae) on these plots. Their presence, along with the chrysomelid larvae, may explain why predaceous soil arthropods (mostly larvae of soldier, carabid and staphylinid beetles) were more common in unburned plots. Microarthropods (mostly mites and collembolans) which feed mainly on litter and fungi, were also more abundant on unburned sites (Seastedt 1984b). Somewhat surprisingly, millipedes were more abundant on burned plots. These arthropods are believed to feed primarily on foliar litter and were expected to be more common on unburned plots. This group showed a very strong increase in biomass over the sampling dates, and the temporal response strongly suggested that food resources govern their densities. Millipedes are relatively mobile, however, and different results among treatments may have resulted from preferences for over-wintering habitats rather than a correlation with resource availability of the surrounding few meters of prairie.

Soil arthropods compose a large and diverse component of the fauna of tallgrass prairie. Results presented here indicate that the amount of arthropod biomass in tallgrass prairie is several times to an order of magnitude larger than amounts found in either mixed-grass or shortgrass prairie (e.g., McDaniel 1971, Lloyd and Kumar 1977). Our findings indicate that year-to-year variations in the productivity of the tallgrass prairie can influence both the densities and trophic composition of this fauna, but a lag-time of a year or more occurs between the plant and arthropod response. Important indicator species of the relative vigor of the tallgrass prairie include the cicadas, which may be positively correlated with root xylem activity, and the white grubs, whose numbers and biomass appear related to both the amounts and nitrogen concentrations of roots and rhizomes. The difference in feeding activities of these two belowground herbivore groups explains why only the latter group is an acknowledged "pest" species. A decline in plant productivity (specifically, a decline in root xylem volume) will likely result in a decline in cicada numbers. However, a decline in the survivorship of roots and rhizomes likely results in a period of increased survivorship and growth of white grubs due to increased nitrogen content of the food resource. Outbreaks of white grubs can therefore be expected following several years of drought or on sites that have been stressed for several years due to overgrazing or excessive mowing.

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BEE-FLOWER INTERACTIONS ON AN OLD FIELD IN SOUTHEASTERN MICHIGAN

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Abstract. The mid-successional community of a 7.7 ha abandoned field surrounded by oak-hickory woods contained 57 species of native and naturalized flowers that were visited by 134 species of bee (including the introduced honey bee) in the 1972 and 1973 seasons. Flowering lasted from late April-early May to October, for 160 days in 1972, 171 days in 1973.

Nineteen "principal resource" flower species were abundant and broadly polyphilic, being visited by 28-49 bee species each. A few common or conspicuous flowers (*Rumex acetosella, Euphorbia corollata, Lithospermum croceum*) attracted few bees but were visited frequently by other insects.

Eleven bee species visited 14-39 flower species each; most of the others were moderately polytropic, but a few restricted their visitation to closely related taxa, including 10 species limited to *Solidago* and 4 species to *Compositae-Cynareae*, and two bees were found only on a single flower species each (*Dufourea monardae* on *Monarda fistulosa* and *Andrena rudbeckiae* on *Rudbeckia hirta*). Honey bees visited many flower species but ignored the bloom of some common ones (*Potentilla inclinata, Chrysanthemum leucanthemum, Solidago juncea*).

Flowering periods ranged from 15 days or less (*Crataegus crus-galli*) to 50 days or more (*Potentilla inclinata, Hypericum perforatum, Chrysanthemum leucanthemum*). These periods overlapped extensively, and 15-28 principal resource species were in bloom each 15-day interval from May 20 to September 1. Flight periods of native bees ranged from 17 (*Andrena rudbeckiae*) to 154 (*Ceratina dupla*) days; they also overlapped, and 32-61 species of bee were in flight per 15-day interval from May 5 to September 1.

Although numbers of bee species visiting floral resources in the course of the season were not closely correlated with resource diversity, the number per flower species was greatest early and late in the season, when there were relatively few flowers in bloom. The percentage of available bee species that visited a given flower species was greater for principal resources than for less important ones. Most of the flowers appeared to be adapted for visitation by many different bee taxa.

The pollen loads of polytropic bees often contained pollen from 3-4 species other than the one at which the bee was collected and occasionally from plants that did not occur on the field. Mixed loads were rare in bees that restricted visitation to a few flower species.

Within the last decade the open area of the field has been reduced, populations of some of the principal resource flowers have declined, and some woody species with short flowering periods have appeared. Eventually the flora is likely to approach that of the adjacent woodland community which supports a number of spring-flowering herbs but provides little bloom later on in the season. A less diverse bee fauna seems likely to characterize the field in the future.

INTRODUCTION

The observations reported here were made in the course of a long-term (1949-84) study of successional changes in the flora and fauna of a 7.7 ha abandoned field at the Edwin S. George Reserve, Livingston County, Michigan. This field, an open tract surrounded by oak-hickory woods, was probably cleared before 1850, then cultivated until 1925-26, since when it has not been subject to fires, grazing (except by deer, *Odocoileus virginianus*), or man-made disturbance of soil or vegetation (Evans 1975). For most of the study period, it has supported a prairie-like grassland with many species of flowering plants providing resources of pollen and nectar for bees and other insects. A detailed account of the relations between the flora and its bee visitors is in preparation. This paper is a preliminary report, focussing on the flowering seasons of 1972-73, when the diversity and abundance of bloom appeared to be at particularly high levels (72 species of herbs and 4 species of shrubs were recorded in flower) and when a concentrated effort was made to observe bee-flower interactions throughout the entire flowering season. Some additional records made in more recent years have been included to provide a more complete picture.

METHODS

Flower species were identified in the field after voucher material had been determined at the University of Michigan Herbarium. The field's flora was periodically inventoried, and records of the dates and duration of flowering were made at frequent intervals (in 1972-73, on 2-3 days every week) throughout the flowering season. Flower abundance was not generally quantified but was assessed visually in terms of limited or widespread occurrence and of conspicuousness, especially at the time of peak bloom. Observation of visitation by bees was usually made between 9:00 a.m. and 4:00 p.m. and on any given day was limited to a maximum of 30-40 minutes per flower species. Because of the need to shift attention from one resource to another as these were encountered in the field, changing from day to day in the course of the season, no orderly system of monitoring was developed. More attention was given to abundant resources when they were being heavily visited than was paid to them near the beginning or end of their flowering periods or to less frequently encountered species. It has not been possible to express the data in such terms as the numbers of bee visits per unit sampling effort on each flower species, and therefore statistical treatment has not been attempted.

Study of the bee fauna began with a preliminary survey by U.N. Lanham in 1957-58; he collected 81 species. In 1972-73, 134 species were taken. By 1984, 172 species had been recorded, of which 157 have been reported at one or more of 64 species of flower. The rapid movement of most bees and the small size of many species necessitated their collection for identification, but as familiarity with the bee fauna increased some species could be recognized without capture; an effort was made to avoid excessive removal of *Bombus* spp. and of oligotropic species, e.g., *Andrena rudbeckiae* and *Dufourea monardae*. Voucher specimens were taken with a net, placed in separate collecting tubes for each floral resource, and tentatively identified in the laboratory from keys and descriptions given in Mitchell (1960, 1962); they were subsequently submitted to specialists for corrected determination. Records were kept of the date of capture, the species of flower visited, and, when possible, the bee's behavior in gathering pollen and/or probing for nectar. Samples from pollen loads of selected bee visitors were transferred to glass slides, placed in glycerine jelly stained with fast green, and examined microscopically under high power; 200-300 pollen grains were generally counted from each sample. The assembled bees are in the author's collection, which will be placed in the University of Michigan Museum of Zoology.

The nomenclature of the plants reported follows that of Voss (1972, 1985) as far as possible and that of Fernald (1950) for the remainder except for the use of *Hieracium piloselloides* (see Voss and Böhlke 1978). Bee nomenclature follows that of Krombein, Hurd, Smith and Burks (1979).

THE FLORAL RESOURCES OF 1972-73

Bee visitation has been recorded for 57 species of flower that were observed in bloom in the 1972 and 1973 seasons. These

were distributed among 16 families (Table 1), consisting principally of Compositae (25 spp.), Rosaceae (9 spp.), and Leguminosae (6 spp.). The majority were indigenous species, but 17 were naturalized from Europe, several of which were fairly recent arrivals on the field: *Hieracium piloselloides* in 1963, *Carduus nutans* in 1966-67, *Centaurea maculosa* in 1969, *Cirsium arvense* in 1973. All of the plants had small flowers (the maximum corolla spread was 20-30 mm, in *Fragaria* and *Rubus*), but these were generally displayed in units of larger size: heads (*Hieracium, Monarda, Carduus, Cirsium*), panicles (*Solidago*), cymes (*Potentilla, Hypericum*), or umbels (*Asclepias*). Several structural blossom-types (Faegri and van der Pijl 1979) were represented: the dish- or bowl-shaped (*Fragaria, Potentilla*), the brush-shaped (*Antennaria, Carduus*), the disk-shaped (*Chrysanthemum, Rudbeckia*), and the flag-shaped (*Lespedeza, Desmodium*) -forms that pose differing problems for securing pollen and nectar. The predominant flower colors were yellow (22 spp.), white (15 spp.) and purple-pink (14 spp.); orange (2 spp.), blue (1 sp.), and greenish (3 spp.) flowers were also present, but no red flowers (all bees are regarded as red-blind, Proctor and Yeo 1972) were encountered. Most of the flower species present provided both pollen and nectar for bee visitors. However, the field's populations of *Antennaria fallax* and *A. neglecta*, both of which are dioecious, consisted almost wholly of pistillate individuals, producing no pollen, so that these early-season flowers were resources for nectar only. Since bees are not able to collect and utilize the pollinia of *Asclepias* for provisions, both *A. tuberosa* and *A. syriaca* must also have been visited only for nectar. In contrast, *Hypericum perforatum* seemed to produce little if any nectar (this was originally noted by Müller 1883) and appeared to be visited chiefly if not entirely for pollen. (Few of the flowers were large enough to facilitate measurement of nectar content, and no assessment of nectar production or flow was made.)

Flower species were categorized as (1) ''principal resources'' if their bloom was widespread and abundant over the field, conspicuous (to the observer) at the time of peak flowering, and heavily visited by bees; (2) ''supplemental resources'' if their bloom was either less abundant and conspicuous or less heavily visited (not only in terms of numbers of bee species attracted but also with respect to the numbers of bee visits recorded); and (3) ''subsidiary resources'' if only a low level of visitation (not more than 7 spp. of bee visitors nor more than 25 bee-visits recorded) was indicated. As shown in Table 1, nineteen species qualified as principal resources, each being visited by at least 28 (maximum, 49) species of bees and providing records of at least 100 (maximum, 506) bee visits; each had at least 2 (maximum, 12) species regarded as ''frequent visitors'' (defined here by 10 or more records of visitation). Of the 157 species of bee that were recorded as flower vistors, 148 have been taken at one or more of the principal resources.

Twelve flower species, each visited by only 10-21 species of bees and yielding fewer than 72 bee visits, were considered supplemental resources. Several of these (*Lespedeza virginica, Erigeron strigosus, Achillea millefolium*) bloomed widely and abundantly on the field but, as indicated in Table 1, yielded considerably fewer bee visit records than did any of the principal resource species. The native composite *Liatris aspera*, with 19 spp. of bee visitors and 126 bee visits recorded, is conservatively placed as a supplemental resource; it was visited frequently, however, by *Bombus* spp. and by *Apis*, and was generally widespread and abundant in late summer when the number of principal resources was small. Eighty bee species were recorded at supplemental resources, including 7 uncommon species not taken at principal resources.

The remaining 25 species of flower that bloomed in the 1972-73 seasons have provided little evidence of significant utilization by bees. They included three species (*Rumex acetosella, Lespedeza capitata, Euphorbia corollata*) that were both widespread and abundant but that, despite extensive monitoring, failed to show much bee visitation. Several species in this subsidiary resource category (*Spiraea alba, Aster azureus, A. lateriflorus, Cirsium discolor*) which generally attract bees when abundant were represented on the field by very few individual plants and thus produced a very small amount of bloom. Several others (*Desmodium marilandicum, D. sessilifolium, Tragopogon pratensis, Lactuca canadensis, Hieracium longipilum*) were often grazed on by deer so heavily that their flowering was severely diminished. As a group, these subsidiary resources were visited by 51 species of bee; one such resource, *Physalis heterophylla*, provided the only record of *Colletes latitarsis* obtained on the field.

TABLE 1. The floral resources for bees on Evans Old Field, Livingston County, Michigan, in 1972-73. Numbers of bee species visiting, and numbers of bee visits recorded, are given in parentheses.

1. ''Principal resource'' species (abundant, conspicuous, heavily visited):

ROSACEAE — *Rubus flagellaris* (45-144), *Crataegus crus-galli* (31-133), *Fragaria virginiana* (49-506), *Potentilla inclinata* (40-310). GUTTIFERAE — *Hypericum perforatum* (35-199). ASCLEPIADACEAE —*Asclepias tuberosa* (32-142). LABIATAE —*Monarda fistulosa* (32-417). RUBIACEAE —*Houstonia longifolia* (34-232). COMPOSITAE — *Solidago juncea* (36-188), *S. nemoralis* (40-196), *S. rigida* (41-266), *Antennaria neglecta* (33-101), *A. fallax* (28-130), *Rudbeckia hirta* (33-165), *Chrysanthemum leucanthemum* (29-102), *Carduus nutans* (34-243), *Centaurea maculosa* (34-145), *Hieracium aurantiacum* (45-365), *H. piloselloides* (36-278).

2. ''Supplemental resource'' species (less abundant and/or less heavily visited):

LILIACEAE — *Asparagus officinalis* (10-58). ROSACEAE — *Potentilla arguta* (13-51), *P. simplex* (15-60), *P. recta* (15-60). LEGUMINOSAE — *Trifolium repens* (13-66), *Lespedeze virginica* (10-54). ASCLEPIADACEAE — *Asclepias syriaca* (19-60). COMPOSITAE — *Liatris aspera* (19-126), *Erigeron strigosus* (14-22), *Achillea millefolium* (21-57), *Cirsium vulgare* (20-61), *C. arvense (19-71), Taraxacum officinale* (15-41).

3. ''Subsidiary resource'' species (mostly rare or with little bloom, few visits recorded):

POLYGONACEAE - *Rumex acetosella* (5-25). ROSACEAE — *Spiraea alba* (4-6), *Potentilla argentea (4-6). LEGUMINOSAE — Desmodium marilandicum (2-2), D. sessilifolium* (3-5), *Lespedeza hirta* (7-24), *L. capitata* (5-10). OXALIDACEAE — *Oxalis stricta* (7-15). POLYGALACEAE — *Polygala polygama (4-4). EUPHORBIACEAE — Euphorbia corollata* (3-3). ONAGRACEAE — *Oenothera fruticosa* (6-12), *O. biennis* (1-2). ASCLEPIADACEAE — *Asclepias viridiflora (1-1). BORAGINACEAE — Lithospermum croceum* (2-2). LABIATAE — *Hedeoma hispida* (3-4). SOLANACEAE — *Physalis heterophylla* (2-3). SCROPHULARIACEAE — *Verbascum thapsus* (2-3). COMPOSITAE — *Aster azureus* (2-3), *A. lateriflorus* (1-1), *Gnaphalium obtusifolium* (2-2), *Cirsium discolor* (2-4), *Krigia virginica* (3-7), *Tragopogon pratensis* (3-16), *Lactuca canadensis* (1-1), *Hieracium longipilum* (1-1).

THE FLOWERING SEASON

In 1972 and 1973, the flowering season, as estimated from the appearance of the first open flowers in the spring (*Antennaria neglecta*) to the last flowers producing pollen and nectar in the fall (*Solidago nemoralis*), lasted for 160 days (May 4 - October 10) and 171 days (April 24 - October 12), respectively. Despite an unusually late killing frost on June 9, 1972, the two seasons were nearly identical in the sequence and duration of flowering of most of the resource species; these features for the 1973 season are shown in Fig. 1 for the principal resources. The length of the flowering period of individual species varied considerably: two species (*Crataegus, Rubus*), both shrubs, had short flowering periods of approximately 15 days each, six species (*Potentilla, Hypericum, Houstonia, Rudbeckia, Chrysanthemum, Carduus*) flowered for

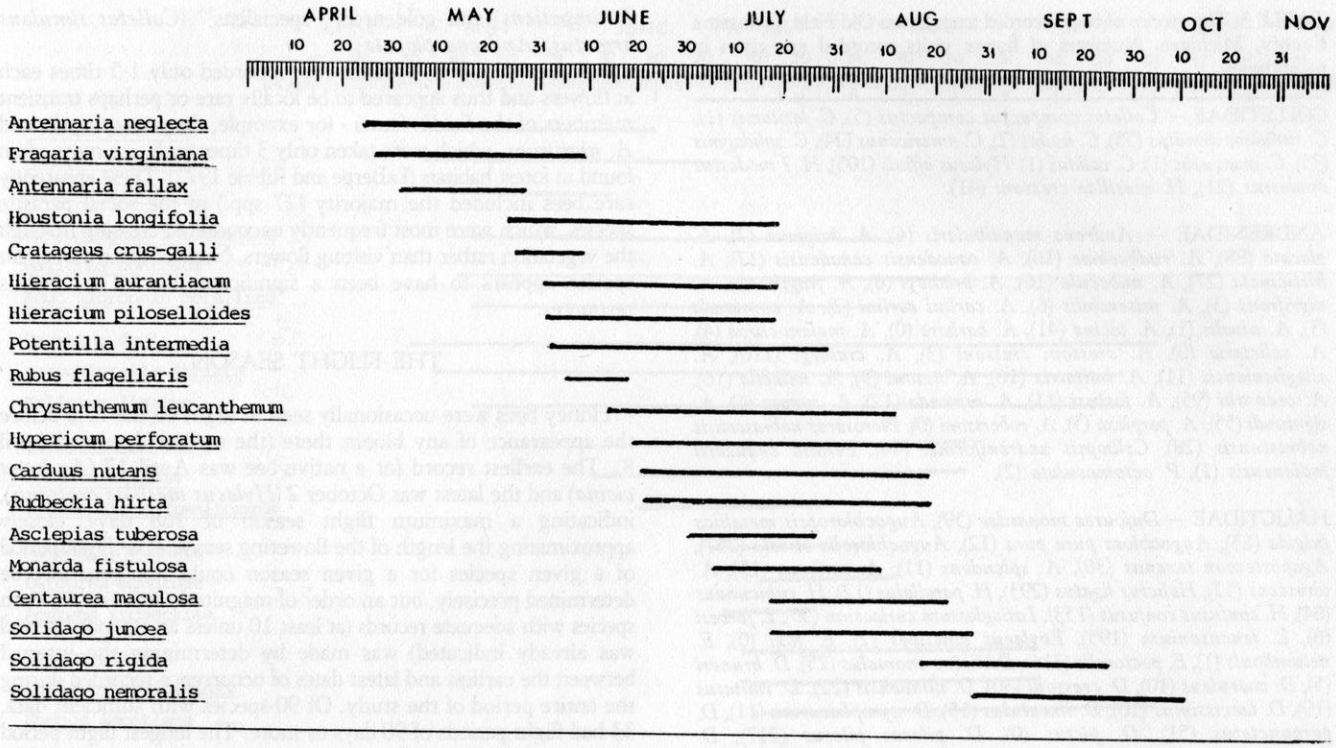

FIG. 1. Seasonal progression of flowering periods in 1973 for species serving as principal resources for bees on Evans Old Field, Livingston County, Michigan.

50 or more days each, and the remainder lasted from 3-6 weeks each. As in many other temperate-zone plant communities, seasonal patterns in flowering were evident: among the principal resources, several species (*Antennaria* 2 spp., *Fragaria*) limited their bloom to the spring, others (*Solidago* 2 spp.) to the late summer and early fall, and some (*Asclepias, Monarda*) to mid-summer. There was much overlap in flowering periods, however, and a commonly observed staggered sequence of bloom was evident, such that a number of resources were available to bees at any given time over a large part of the flowering season. Table 2 shows the numbers of principal resource and other bee-visited species that were in bloom in each of the successive 15-day intervals of the flowering seasons of 1972 and 1973. Although comparatively few species (9 or fewer) were available at the beginning and end of the season, from 15 to 28 were in bloom in each interval from May 20 to September 1; the greatest diversity occurred in July and early August. This continued high diversity does not of itself, however, guarantee an ongoing abundance of bloom. Indeed, the available records suggest that most of the principal resource species that began to flower early in the summer had either completed or passed the peak of their bloom by late July, whereas those which had their peak bloom at the end of the summer did not begin to flower until mid-August or later. The general impression was of a decreased abundance of bloom from the latter part of July to the middle of August. Ginsberg (1983) found evidence of a midsummer decline in flower abundance in an old-field community in central New York State.

TABLE 2. Numbers of species of bee-visited flowers blooming on Evans Old Field in successive 15-day periods of the season. (Based on data for 1972 and 1973).

	Number of flower species recorded in bloom		
Period	Principal resource species	Other species	Total species
1. May 5-19	4	3	7
2. May 20-June 3	8	7	15
3. June 4-18	8	13	21
4. June 19-July 3	9	14	23
5. July 4-18	12	14	26
6. July 19-August 2	11	16	27
7. August 3-17	9	19	28
8. August 18-Sept. 1	4	13	17
9. Sept. 2-16	2	7	9
10. Sept. 17-Oct. 1	2	4	6
For the entire season	19	38	57

THE BEE FAUNA

The bee species recorded from the field (Table 3) represent about 40 percent of the total number reported from the State of Michigan by Mitchell (1960, 1962) and are distributed by family as follows: Colletidae (11), Andrenidae (35), Halictidae (44), Megachilidae (30), Anthophoridae (37), and Apidae (15). The most prominent genera present were *Andrena* (31 spp.), *Dialictus* (15 spp.), *Nomada* (14 spp.), *Megachile* (11 spp.), *Bombus* (11 spp.), *Sphecodes* (10 spp.), *Colletes* (8 spp.), *Melissodes* (8 spp.) and *Osmia* (7 spp.). Except for the honey bee *Apis mellifera* and perhaps *Andrena wilkella* (see LaBerge 1964:306), all of the field's bees were native North American species. They ranged in size (body length) from 3.5-4 mm (*Hylaeus mesillae cressonii*) to 20-25 mm (queens of *Bombus nevadensis auricomus*); 37 species were less than 7 mm in length but the majority were of medium size (10-15 mm). They are divided almost equally between the so-called "long-tongued" and "short-tongued" bees. Forty-one species were social parasites that live in the nests of host bees and do not collect pollen to provision their young.

Twenty-seven species were observed at flowers 50 or more times each, accounting for 73.4 percent of the 5,422 flower visits that were recorded. With the exception of *Dufourea monardae*, to which special attention was paid because of its monotropic habits and its recent extension of range into Michigan (Bouseman 1976), all were regarded as major uses of the field's resources. The most abundant/active bee was clearly *Apis mellifera* (780 flower visits recorded), colonies of which were maintained on farms within 1-2 km of the field and which probably also nested as wild bees in

TABLE 3. The species of bees recorded from Evans Old Field, Livingston County, Michigan. Numbers of flower visits recorded are given in parentheses.

COLLETIDAE — *Colletes compactus compactus* (5), *C. latitarsis (1), C. simulans armatus* (55), *C. nudus* (2), *C. americanus* (24), *C. solidaginis* (35), *C. inaequalis* (1). *C. validus* (1). *Hylaeus affinis* (105), *H. ? modestus modestus* (21), *H. mesillae cressoni* (41).

ANDRENIDAE — *Andrena mandibularis* (4), *A. krigiana* (2), *A. placata* (88), *A. rudbeckiae* (16), *A. canadensis canadensis* (17), *A. hirticincta* (27), *A. nubecula* (16), *A. bradleyi* (0), *A. fragilis* (3), *A. nigrifrons* (3), *A. miserabilis* (6), *A. carlini carlini* (2), *A. commoda* (3), *A. nivalis* (1), *A. vicina* (41), *A. barbara* (0), *A. melanochroa* (4), *A. salictaria* (0), *A. cressoni cressoni* (3), *A. crataegi* (110), *A. alleghaniensis* (11), *A. imitatrix* (16), *A. nasoni* (9), *A. wilkella* (16), *A. ceanothi* (95), *A. forbesi* (11), *A. miranda* (12), *A. rugosa* (6), *A. sigmundi* (55), *A. perplexa* (5), *A. robertsoni* (0), *Pterosarus nebrascensis nebrascensis* (28), *Calliopsis andreniformis* (40), *Perdita bequaerti indianensis* (1), *P. octomaculata* (2).

HALICTIDAE — *Dufourea monardae* (59), *Augochloropsis metallica fulgida* (63), *Augochlora pura pura* (12), *Augochlorella striata* (257), *Agapostemon texanus (30), A. splendens* (11), *A. sericeus* (15), *A. virescens* (52), *Halictus ligatus* (293), *H. parallelus* (12), *H. rubicundus* (64), *H. confusus confusus (153), Lasioglossum coriaceum* (50), *L. forbesi* (6), *L. leucozonium* (195), *Evylaeus cinctipes* (2), *E. foxi* (0), *E. nelumbonis* (1), *E. pectoralis* (316), *Dialictus anomalus* (25), *D. bruneri* (5), *D. coeruleus* (10), *D. cressoni* (30), *D. illinoensis (22), D. imitatus* (19), *D. laevissimus* (10), *D. lineatulus* (15), *D. nymphaearum* (11), *D. perpunctatus* (51), *D. pictus* (0), *D. pilosus pilosus* (217), *D. supraclypeatus* (16), *D. tegularis* (14), *D. vierecki* (91), *Sphecodes confertus* (3), *S. cressoni* (4), *S. davisi* (0), *S. dichrous* (11), *S. heraclei* (2), *S. illinoensis* (0), *S. knetschi* (0), *S. persimilis* (0), *S. ranunculi* (2), *S. stygius* (14).

MEGACHILIDAE — *Stelis vernalis* (1), *Heriades leavitti* (23), *H. carinata* (66), *Hoplitis cylindrica* (3), *H. albifrons albifrons (1), H. pilosifrons* (71), *H. producta producta* (2), *Osmia lignaria lignaria* (3), *O. georgica* (4), *O. texana* (8), *O. distincta* (3), *O. pumila* (46), *O. atriventris* (16), *O. simillima* (3), *Megachile brevis brevis* (35), *M. mendica mendica* (50), *M. texana* (1), *M. inermis* (14), *M. montivaga* (13), *M. relativa* (16), *M. addenda* (4), *M. latimanus* (94), *M. albitarsis* (0), *M. frugalis frugalis* (1), *M. pugnata pugnata* (15), *Chalicodoma campanulae campanulae* (5), *Coelioxys octodentata* (9), *C. rufitarsis* (19), *C. alternata* (3), *C. modesta* (1).

ANTHOPHORIDAE — *Holcopasites calliopsidis calliopsidis* (7), *Epeolus bifasciatus bifasciatus* (1), *E. ? interruptus* (2), *E ? lanhami* (1), *E. pusillus* (11), *E. scutellaris* (18), *Triepeolus cirsianus* (2), *T. ? cressoni cressoni* (0), *T. simplex* (2), *Nomada ? armatella* (1), *N. cressoni cressoni* (40), *N. pygmaea* (24), *N ? sayi* (1), *N. vicina vicina* (4), *N. ? lepida* (0), *N. maculata* (13), *N. ? ovata* (1), *N ? perplexa* (2), *N. bishoppi* (0), *N. colorata* (1), *N. subrutila* (2), *N ? vincta vincta* (0), *N ? articulata* (3), *Melissodes communis communis* (13), *M. desponsa* (35), *M. dentiventris* (2), *M. nivea* (8), *M. rustica* (7), *M. subillata* (11), *M. tincta* (4), *M. wheeleri* (1), *Anthophora abrupta* (1), *A. walshi* (1), *A. furcata terminalis* (6), *Ceratina calcarata*, male (2), *C. dupla* (336), *Xylocopa virginica virginica* (2).

APIDAE — *Bombus affinis* (34), *B. terricola terricola* (6), *B. nevadensis auricomus* (33), *B. griseocollis* (38), *B. bimaculatus* (154), *B. impatiens* (60), *B. perplexus* (25), *B. vagans* (45), *B. borealis* (5), *B. fervidus fervidus* (22), *B. pennsylvanicus pennsylvanicus* (7), *Psithyrus ashtoni* (14), *P. citrinus* (5), *P. fernaldae* (3), *Apis mellifera (779).*

the adjacent woods; as its numbers built up through reproduction during the summer and as floral resources increased, *Apis* was on many days the predominant bee visitor on the field. Also abundant were several early season andrenids (*Andrena ceanothi, A. crataegi, A. sigmundi*); later on, a number of very small bees (*Hylaeus affinis, Evylaeus pectoralis, Dialictus pilosus, Augochlorella striata, Ceratina dupla*); and towards the end of the summer, several species of bumblebee (*Bombus bimaculatus, B. impatiens*) and goldenrod "specialists" (*Colletes simulans armatus, Andrena placata*).

In contrast, 62 bee species were recorded only 1-5 times each at flowers and thus appeared to be locally rare or perhaps transient members of the field's fauna - for example, *Andrena fragilis* and *A. nigrifrons*, which were taken only 3 times each, are more often found in forest habitats (LaBerge and Ribble 1972). These apparently rare bees included the majority (27 spp.) of the social parasite species, which were most frequently encountered cruising through the vegetation rather than visiting flowers. None of these infrequent species appears to have been a significant user of the field's resources.

THE FLIGHT SEASON

Honey bees were occasionally seen in flight on the field before the appearance of any bloom there (the earliest date was April 8). The earliest record for a native bee was April 17 (*Andrena vicina*) and the latest was October 2 (*Hylaeus mesillae cressonii*), indicating a maximum flight season of 168 days, closely approximating the length of the flowering season. The flight period of a given species for a given season could not generally be determined precisely, but an order-of-magnitude estimate for each species with adequate records (at least 10 unless an extended period was already indicated) was made by determining the interval between the earliest and latest dates of occurrence recorded during the entire period of the study. Of 90 species with sufficient data, 33 had flight periods of 90 days or more. The longest flight period was that of *Apis* (175 days), but 18 native species - all of them halictines except *Ceratina dupla* and including some of the smallest bees on the field (*Dialictus, Augochlorella, Evylaeus*) - had estimated flight periods of 120-154 days. In contrast, the flight period of 16 species was estimated at 30 days or less; all of the records of *Andrena rudbeckiae*, for example, were obtained within a span of 17 days. The only halictid in this category was *Dufourea monardae*, which was limited on the field to visiting a single resource (*Monarda fistulosa*); the other bees with short flight periods were for the most part either early season andrenids and colletids or late season specialists on goldenrods or other composites. An intermediate group of bees, including most of the species of *Bombus, Megachile*, and *Melissodes*, had estimated flight periods ranging from 35 to 88 days.

Fig. 2 provides examples of long, short and intermediate flight periods for selected species. It also illustrates the various seasonal patterns that were noted in the bees' foraging phenologies: (1) flight periods covering most of the flowering season (*Halictus ligatus, Augochlorella striata, Ceratina dupla*); (2) flight periods limited to spring and early summer, i.e., to May-June (*Andrena ceanothi, A. crataegi, A. sigmundi*); (3) flight periods limited to summer, i.e., to late June-early August (*Andrena rudbeckiae,*

TABLE 4. Number of species of bees visiting flowers on Evans Old Field in successive periods of the season. (Based on data for 1972 and 1973).

	Number of bee species			
Period	Taken 50 or more time each	Others	Total	No. spp. per fl.sp. in bloom
1. May 5-19	15	26	41	5.86
2. May 20-June 3	15	22	37	2.47
3. June 4-18	19	42	61	2.90
4. June 19-July 3	20	19	39	1.70
5. July 4-18	21	30	51	1.96
6. July 19-Aug. 2	18	25	43	1.59
7. Aug. 3-17	14	18	32	1.14
8. Aug. 18-Sept. 1	13	27	40	2.35
9. Sept. 2-16	6	23	29	3.22
10. Sept. 17-Oct. 1	5	14	19	3.17
For the entire season	27	107	134	2.35

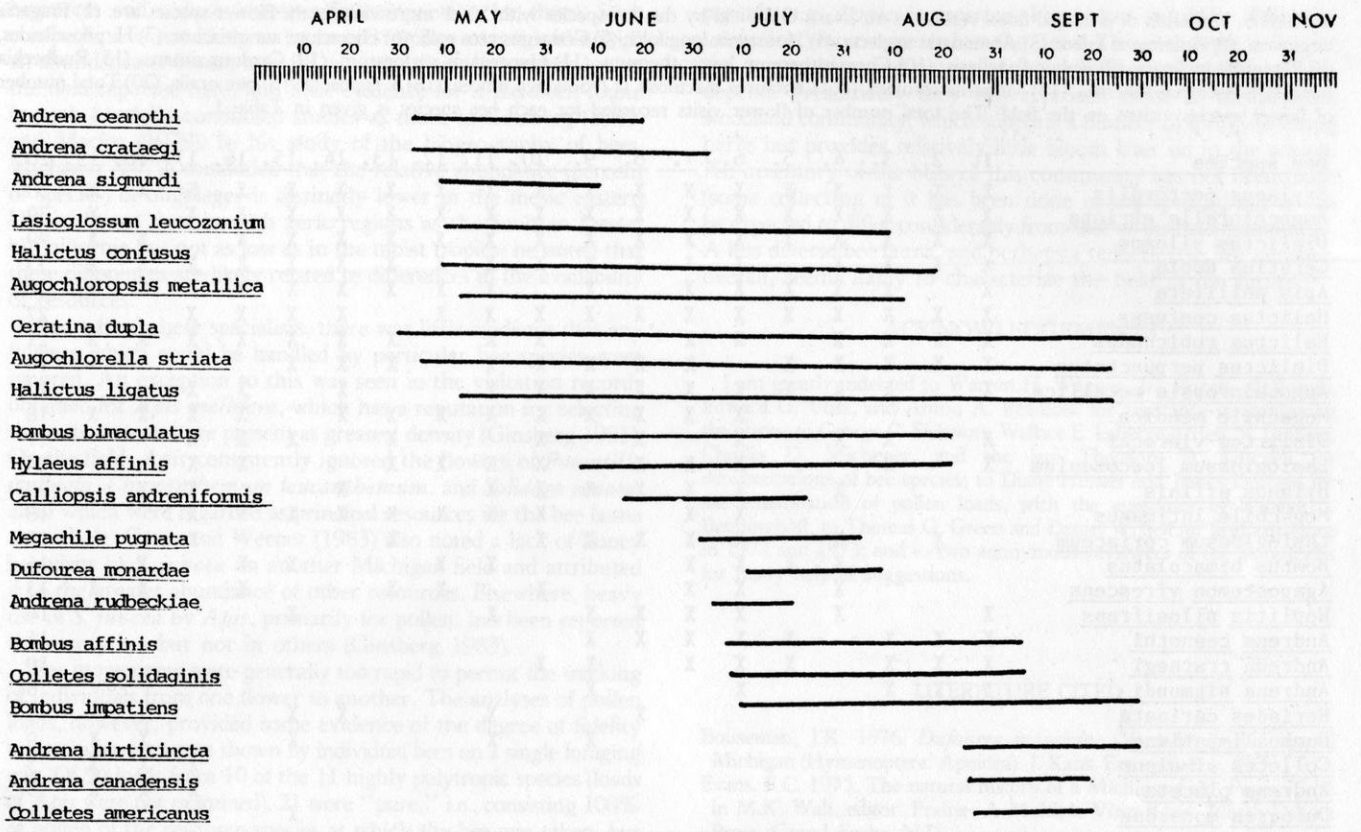

FIG. 2. Estimated maximum duration of flight periods of selected bee species on Evans Old Field, Livingston County, Michigan, based on earliest and latest dates of occurrence.

TABLE 5. Comparative success of floral resources in attracting bees on Evans Old Field, Livingston County, Michigan.

Floral resource	Flowering period (composite 1972–73	Number of bee species Visiting	Available	Percent visiting
PRINCIPAL				
Antennaria neglecta	April 24–May 24	33	66	50.0
Fragaria virginiana	April 25–June 11	49	75	65.3
Antennaria fallax	May 1–May 26	28	68	41.2
Houstonia longifolia	May 24–July 19	34	114	29.8
Crataegus crus-galli	May 25–June 7	31	66	47.0
Hieracium piloselloides	June 1–July 19	36	118	30.5
Hieracium aurantiacum	June 1–July 21	45	121	37.2
Potentilla inclinata	June 1–July 28	40	116	34.5
Rubus flagellaris	June 4–June 16	45	79	47.0
Chrysanthemum leucanthemum	June 12–August 9	30	97	30.9
Hypericum perforatum	June 19–August 16	35	92	38.0
Carduus nutans	June 20–August 17	34	92	37.0
Rudbeckia hirta	June 20–August 17	33	92	35.0
Asclepias tuberosa	June 29–July 26	32	79	40.5
Monarda fistulosa	July 6–August 10	32	82	39.0
Centaurea maculosa	July 17–August 23	34	54	63.0
Solidago juncea	July 18–August 29	36	81	44.4
Solidago rigida	August 18–September 20	41	73	56.2
Solidago nemoralis	August 29–October 10	40	58	69.0
OTHERS				
Erigeron strigosus	June 14–August 22	14	105	13.3
Euphorbia corollata	July 17–August 25	3	77	4.0
Lespedeza virginica	August 22–August 31	10	57	17.5

TABLE 6. Visitation of principal floral resources on Evans Old Field by the bee species with 50 or more visits each. Flower species are: (1) Fragaria virginiana, (2) Antennaria fallax, (3) Antennaria neglecta, (4) Houstonia longifolia, (5) Crataegus crus-galli, (6) Hieracium aurantiacum, (7) H. piloselloides, (8) Potentilla inclinata, (9) Rubus flagellaris, (10) Chrysanthemum leucanthemum, (11) Hypericum perforatum, (12) Carduus nutans, (13) Rudbeckia hirta, (14) Asclepias tuberosa, (15) Monarda fistulosa, (16) Centaurea maculosa, (17) Solidago juncea, (18) S. rigida, (19) S. nemoralis. (20) Total number of flower species visited on the field. The total number of flower visits recorded for each bee species is given in Table 1.

Bee species	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.	18.	19.	20.
Evylaeus pectoralis	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	30
Augochlorella striata	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	39
Dialictus pilosus	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	29
Ceratina dupla	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	33
Apis mellifera	X		X	X	X	X	X		X		X	X	X	X	X	X		X	X	28
Halictus confusus	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X			27
Halictus rubicundus	X	X	X	X		X	X			X	X		X	X	X	X	X	X	X	21
Dialictus perpunctatus	X	X	X	X	X		X	X	X	X	X		X	X	X					14
Augochloropsis metallica	X		X	X	X	X	X	X	X	X	X			X		X	X			17
Megachile mendica						X	X	X	X	X	X	X	X	X		X	X	X	X	18
Dialictus vierecki	X		X	X		X		X		X			X		X	X	X			17
Lasioglossum leucozonium	X		X			X	X	X		X	X	X	X			X	X			24
Hylaeus affinis				X		X	X	X	X	X	X			X			X	X		20
Megachile latimanus						X	X			X	X	X	X	X	X	X	X			18
Lasioglossum coriaceum		X		X		X	X	X	X	X			X				X			15
Bombus bimaculatus				X	X	X	X				X	X			X	X		X		16
Agapostemon virescens				X		X	X			X		X	X			X		X	X	13
Hoplitis pilosifrons	X			X		X	X	X	X		X				X					16
Andrena ceanothi	X	X	X		X	X	X	X	X											14
Andrena crataegi	X	X	X		X	X	X		X	X										10
Andrena sigmundi	X	X	X			X			X											6
Heriades carinata								X			X			X	X					7
Bombus impatiens									X		X				X			X	X	9
Colletes simulans																	X	X	X	3
Andrena placata																	X	X	X	3
Dufourea monardae															X					1

Dufourea monardae, Megachile pugnata); (4) flight periods limited to late summer and early fall, i.e., to late August-September (*Colletes americanus, Andrena candensis, A. hirticincta*).

As with the flowering periods of the plants, the flight periods of the bees can be arranged in a staggered sequence through the flight season, with much overlapping. Table 4 shows, however, that the species diversity of bee visitors in 1972-73 was maintained a fairly high level for most of the season, varying between 32 and 61 per 15-day interval from May 5 to September 1, with a peak in early summer and a low in the first half of August. Although numbers of bee species visiting floral resources in the course of the season were not closely correlated with resource diversity, the number of bee species per flower species was greatest early and late in the season, when there were relatively few flowers in bloom.

BEE - FLOWER INTERACTIONS

Table 5 compares the success of the 19 principal resource flowers in attracting visitors, in terms of the percent of bee species considered to be available (based on their estimated light periods) during a resource's flowering period that were actually recorded at that resource. These values ranged from 29.8% to 69.0% (considerably higher values than those obtained for most of the supplemental and subsidiary resources, e.g., *Lespedeza virginica*, 17.5%; *Erigeron strigosus*, 13.3%; *Euphorbia corollata*, 4.0%). Highest values were found for species blooming early in the season (*Fragaria, Antennaria*) or toward its close (*Solidago*), while relatively low values prevailed in mid-summer (*Chrysanthemum, Hypericum, Carduus*). Although some of the rare flowers, e.g., *Spiraea alba, Aster azureus, Cirsium discolor*, are known to be attractive to bees when their bloom is abundant, several common or conspicuous species (*Rumex acetosella, Euphorbia corollata, Lithospermum croceum*) also failed to yield many bee records (though they were visited frequently by other insects such as flies and butterflies). Small-flowered plants with low-growing and loosely arranged inflorescences (*Houstonia, Rumex*) were seldom visited by large bees, and the intricate flower structures (the flag-blossom type of Faegri and van der Pijl 1979) of *Lespedeza* and *Desmodium* seemed to discourage visitation by bees other than *Megachile, Bombus* and *Apis*.

Table 6 indicates the principal resources that were visited by the bee species for which 50 or more records are available. Eleven of these were broadly polytropic, visiting 13 or more of the principal resource species and 14-39 of all flower species at which bees were taken. Such a high degree of polytropy was made possible by the long flight periods of these bees. Michener (1979) has pointed out that male bees and females not collecting pollen are not usually very specific in their flower visiting habits. In the present study, field observation of pollen collecting and analyses of pollen loads (see below) indicated that these polytropic bees obtained pollen from most of the flower species which they visited.

In contrast, three of the bee species in Table 6 limited their visitation to very few resources: *Colletes simulans armatus* and *Andrena placata* to the three species of *Solidago* and, as noted above, *Dufourea monardae* to *Monarda fistulosa*. Other bees apparently restricting their visits on this field to a single flower species or to two or three closely related taxa included *Andrena rudbeckiae* on *Rudbeckia hirta*, a group limited to *Solidago* (*Colletes americanus, C. solidaginis, Andrena canadensis, A. hirticincta, A. nubecula, Pterosarus nebrascensis, Melissodes nivea, M. rustica, M. subillata, M. tincta*), and a group limited to *Compositae-Cynareae* (*Osmia texana, Megachile inermis, M. pugnata, Melissodes desponsa*). Most (but not all) of these bees are regarded as oligoleges throughout their geographic ranges, and most were found on the field in the latter part of the season (when the number of available flower species was small). As Michener (1954) has pointed out, oligolecty tends to divide available

resources and reduce interspecific competition for them. Such competition is not likely to be severe in plant communities with an abundance of bloom over an extended flowering season, as on the field reported here, and little evidence for it has been found in such carefully conducted studies as those of Ginsberg (1983) and Macior (1978). In his study of the biogeography of bees, Michener (1979) concluded that the relative abundance (percent of species) of oligoleges is distinctly lower in the mesic eastern United States than in such xeric regions as the Sonoran Desert of California but not as low as in the moist tropics; he noted that these differences are likely related to differences in the availability of resources.

Apart from these specialists, there was little evidence that any flowers which could be handled by particular bee species were ignored. An exception to this was seen in the visitation records obtained for *Apis mellifera*, which has a reputation for selecting the resources that are present at greatest density (Ginsberg 1981). On the field, *Apis* consistently ignored the flowers of *Potentilla inclinata, Chrysanthemum leucanthemum*, and *Solidago juncea*, all of which were regarded as principal resources for the bee fauna as a whole. Gross and Werner (1983) also noted a lack of honey bee visits to *S. juncea* on another Michigan field and attributed it to the greater abundance of other resources. Elsewhere, heavy use of *S. juncea* by *Apis*, primarily for pollen, has been reported in some years but not in others (Ginsberg 1983).

Bee movements were generally too rapid to permit the tracking of individuals from one flower to another. The analyses of pollen loads, however, provided some evidence of the degree of fidelity to particular resources shown by individual bees on a single foraging trip. Of 96 loads from 10 of the 11 highly polytropic species (loads of *Apis* were not examined), 21 were "pure," i.e., consisting 100% of pollen of the resource species at which the bee was taken, but the remaining 75 loads were "mixed" and contained pollen from 3-4 other species in addition to the one at which the bee was collected. The presence in some loads of pollen from plants not occurring on the field (tentatively identified as *Barbarea, Ilex, Cornus, Rhus*, and *Ericaceae*) indicated that some bees had previously visited other areas and habitats and were not restricted to the field's resources. In contrast to these polytropic bees, the individuals of species whose flower visitation on the field was limited to a few resources showed a much higher level of fidelity: of 74 loads examined from 11 species of specialist bees, 68 were "pure." Because fidelity restricts an individual to a particular kind of resource, that bee need not modify its behavior (on a given trip) to handle more than one blossom-type, and this may increase its efficiency as a forager.

CONCLUDING REMARKS

In the course of its historically short development, this small field community has acquired a large and diverse bee fauna. This has been made possible by the accumulation of a species-rich assemblage of herbaceous plants whose varied flowering phenologies have provided substantial supplies of pollen and nectar over an extended annual season. The coexistence of so many species of bees has been facilitated by differences in the timing and duration of their flight periods, by differences in the diversity and kinds of flowers they visited, and by differences in their life cycle characteristics (see Ginsberg 1983). Despite potential disturbance from a large population of honey bee visitors, there has been little evidence of interspecific competition among the native bees. However, the vegetation of the field is now shifting to a shrub stage, in which the total area of open field conditions preferred by many of the currently existing plant species is being steadily reduced; populations of some of the principal resource flowers have declined, and a number of woody species with short flowering periods (e.g., *Lonicera tatarica, Viburnum trilobum, Eleagnus umbellata*) have appeared in the flora. These changes will alter the composition and nature of the resources on which the bees depend. Presumably they will approach those of the adjacent woodland community, which supports a number of spring-flowering herbs but provides relatively little bloom later on in the season. An inventory of the bees of this community has not been made (some collecting in it has been done in the spring), but it can be expected to differ considerably from that of the field community. A less diverse bee fauna, and perhaps a reduction in bee numbers overall, seems likely to characterize the field in the future.

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THE ZOOGEOGRAPHY OF *ANDRENA* FABRICIUS (HYMENOPTERA: ANDRENIDAE) OF THE WESTERN HEMISPHERE

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Abstract. The zoogeography of the North American species of the primarily Holarctic genus *Andrena* (Hymenoptera: Andrenidae) is reviewed. Constraints to distribution of *Andrena* species include moderate oceanic stretches, plant sources of pollen for brood-rearing, edaphic factors affecting nesting sites, the Great Plains, and the glacial episodes in North America. The Great Plains limited the distribution of certain *Andrena* during the interglacial periods of the Pleistocene while the glacial periods separated other species into isolated pockets. Thus a continual opportunity for speciation within the genus is hypothesized.

INTRODUCTION

The bee genus *Andrena* is found on all continents except Australia, Antarctica and South America. It is an Holarctic genus with about 500 species in North America and 650 to 700 species in Eurasia. The relatively few species in Africa south of the Sahara, Central India and Central America are clearly recent derivatives of more northern groups. Even Florida and southern Texas have relatively few species and only one is known from southern Florida.

The genus *Andrena* is a relatively primitive andrenid. Lanham (1949) suggested that the genus *Megandrena*, known from six species from the American Southwest, is more primitive and in many ways intermediate in form between the Australian *Stenotritus* (Colletidae) and the genus *Andrena*. In any case the Andrenidae, and presumably *Andrena*, arose from an early colletid or some primitive melittid (Michener 1944), perhaps in Cretaceous or early Tertiary times.

Several fossil *Andrena* have been described. Two from Baltic amber (lower Oligocene) are referred to the genus *Andrena*, but their affinities among modern species are in doubt. Six species from Florissant shale (Oligocene or Early Miocene) from Colorado seem to be correctly placed in the genus *Andrena* but are not well enough preserved to be placed clearly in any one of the recognized subgenera. Thus, the fossil record provides little aid in determining the origin or phylogeny of the genus *Andrena* except it shows that the genus must have originated early in or before the Tertiary Period. We are dependent upon cladistic analysis of the characters of extant species for information concerning relationships between putative taxa.

Warncke (1967, 1968) reviewed the European species of *Andrena*. Unfortunately, he did not present a clear picture of the phylogeny of the Old World species. He clarified the status of the species and proposed a new subgeneric classification indicating which subgenera he considered to be more primitive in relation to each of the other subgenera. Furthermore, he did not treat the poorly known Asian fauna. Hirashima (1966) revised the Japanese species of *Andrena*, but only a handful of species are presently known from China where a fauna at least equal to that of Europe presumably exists.

The present author and his colleagues (Bouseman and LaBerge 1979, LaBerge 1964, 1967, 1969, 1971, 1973, 1977, 1978, 1980, LaBerge and Bouseman 1970, LaBerge and Ribble 1972, 1975, LaBerge and Hurd 1965, Ribble 1967, 1968, 1974) have been revising the North American species of *Andrena*. Thorp (1969) and his student (Donovan 1977) have revised selected subgenera. In most of these papers a phylogenetic analysis of the species in each subgenus was presented or the species were described in such a way that such an analysis could be readily derived. The relationship of each subgenus to the other subgenera, both North American and Eurasian was also discussed in most of these works. This revision of North American *Andrena* is now nearly completed.

DISTRIBUTION CONSTRAINTS

An interesting aspect of the general distribution of the species of *Andrena* is that few are found on oceanic islands. Great Britain, Japan, Taiwan, and the Canary Islands each have relatively impoverished faunas of *Andrena*. It is evident that even moderate stretches of ocean present barriers to migration for the species of *Andrena*, and that this has been important in the early history of the genus.

Table 1 shows the number of endemic and nonendemic species of *Andrena* found in various regions of the Western Hemisphere. The numbers are based on the 405 species reported in completed sections of the *Andrena* revision. Note that the lowest number of total species, but the highest percentage of endemism occurs in Mexico and Central America. Note also that the next lowest number of species, but the lowest percentage of endemism occurs in the Great Plains. Moderately high endemism and relatively high numbers of species characterize the other four regions. This indicates that the prairie *Andrena* fauna is largely derived from surrounding regions, as has been shown to occur in prairie plants and is also true of birds and mammals (Wells 1970).

The distribution of particular species of *Andrena* in North America is restricted by a number of factors among which food plant preference is of great importance. Many species of *Andrena* are oligolectic, that is, restricted to one or a few plants as pollen sources for their larvae. The distribution of these oligolectic species frequently coincides with the distribution of their pollen sources. For instance, *Andrena erigeniae* Robertson has a known range almost identical with that of Spring Beauty (*Claytonia virginica* L.) on which it depends. That is not to say that any particular woods in which *Claytonia* is blooming will also have *A. erigeniae*, but that *A. erigeniae* is not found where *Claytonia* is absent (Davis and LaBerge 1975).

A few species nest exclusively in sand, rather than loamy soil. For instance, *Andrena* (*Callandrena*) *haynesi* Viereck and Cockerell is found nesting in sand in the prairies and even in sand areas along the Mississippi River in Illinois (Bouseman 1982) and in southeastern Utah in sand dunes (Parker and Griswold 1983). Its distribution is obviously affected by the presence or absence of acceptable nesting substrates. Thus, edaphic requirements can be a factor in limiting the distribution of some species of *Andrena*.

The desert regions of the Southwest and Mexico also have relatively few species of *Andrena* although the number of endemic species appears to be moderately high. The obvious difference

TABLE 1. Distribution of 405 species of Andrena in the Western Hemisphere.

Region	Endemic	Non-endemic	Total	% of endemism
Great Plains	30	48	78	38
Eastern	52	60	112	46
Southwestern	42	46	88	48
Western Montane	83	71	154	54
West Coast	79	64	143	55
Mexico, Central America	35	11	46	78

between the desert regions and the more humid regions to the north and east in North America is the sparseness of the vernal *Andrena* fauna in the desert regions. The relatively high percentage of endemism appears to be due to a radiation of oligolectic species associated with the compositae and certain other plants.

Many species of *Andrena* (*A. crataegi* Robertson, *A. fragilis* Smith, *A. integra* Smith, *A. perplexa* Cresson, and *A. regularis* Malloch, etc.) are adapted to spring-flowering plants and shrubs or trees of the forests or forest margins and are rare or absent in the Great Plains, or desert regions. Occasionally the ranges of species of *Andrena* are split into two parts, an eastern and a western, by the central Great Plains. A few cases occur where the western populations differ from the eastern populations with broad zones of intergradation through the Rocky Mountains, and cases in which the western form must now be considered as a separate, largely allopatric species from its eastern sister species. The Great Plains acts as a barrier to the distribution of vernal, cold-adapted *Andrena* associated with trees and shrubs or associated plants of forests and forest margins. Mengel (1970) discussed the Great Plains as a barrier to distribution of wood warblers.

The Pleistocene glaciations in North America probably were effective, together with ecological factors such as flower preferences, in isolating populations of some species of *Andrena* in the southeast and in the west. This isolation must have lasted long enough to have allowed selection to produce morphological change in at least some populations to the extent of producing sister species. A pair of species in the subgenus *Tylandrena* illustrates this: *Andrena erythrogaster* (Ashmead) is eastern, ranging into the eastern Rocky Mountains; *A. subaustralis* Cockerell is western, ranging from New Mexico and Idaho to the West Coast. The ranges of the two species overlap very little and no hybridization is known to have occurred between them.

In addition, the constriction of the prairies during the greatest expansion of glaciers probably allowed some species of *Andrena*

TABLE 2. Non-Salix, vernal, Nearactic Andrena - 20 species.

A. Species with split ranges (non-prairie):	
A. arabis Robertson	A. perplexa Smith
A. bradleyi Viereck	A. spiraeana Robertson
A. ceanothi Robertson	A. wilmattae Cockerell
A. crataegi Robertson	A. ziziae Robertson
A. nuda Robertson	
B. Species crossing only in the north:	
A. algida Smith	A. nigrihirta (Ashmead)
A. alleghaniensis Viereck	A. persimulata Viereck
A. carlini Cockerell	A. regularis Malloch
A. melanochroa Cockerell	A. thaspii Graenicher
A. milwaukeensis Graenicher	A. vicini Smith
A. miranda Smith	

TABLE 3. Salix visiting, vernal, Nearctic Andrena - 24 species.

A. Crossing prairie only in north:	
A. clarkella (Kirby)	A. sigmundi Cockerell
A. frigida Smith	A. wellesleyana (Robertson)
A. rufosignata (Cockerell)	A. x-scripta (Cockerell)
B. Prairie species:	
A. andrenoides (Ashmead)	A. macoupinensis Robertson
A. commoda Smith	A. mandibularis Robertson
A. cressonii Robertson	A. miserabilis Cresson
A. erythrogaster (Ashmead)	A. nigrae Robertson
A. forbesii Robertson	A. nivalis Smith
A. hippotes Robertson	A. rugosa Robertson
A. illinoiensis Robertson	A. salictaria Robertson
A. imitatrix Cresson	A. tridens Robertson

TABLE 4. Non-Salix, oligolectic Andrena entering the prairies of North America - 17 species.

A. Vernal aestival bees:	
A. geranii Robertson	A. violae Robertson
B. Autumnal/aestival bees:	
A. accepta Viereck	A. lupinorum Cockerell
A. asteris Robertson	A. numbecula Smith
A. brevipalpis Cockerell	A. robertsoni (Dalla Torre)
A. canadensis (Dalla Torre)	A. robervalens Mitchell
A. chromotricha Cockerell	A. rudbeckiae Robertson
A. gardineri Cockerell	A. simplex Smith
A. heliantha Robertson	A. surda Cockerell
A. hirticincta Provancher	

to migrate from east to west or vice versa and to the contrary, the expansion of the prairies since the Wisconsin glaciation seems to have restricted the east-west exchange of populations in several species of *Andrena*.

Forty-four North American *Andrena* species are known to be vernal, polylectic or oligolectic, and more or less transcontinental (that is occurring both in the western mountains and in the eastern forested regions) (Tables 2 and 3). Of these, 24 species use *Salix* as their principal source of pollen for brood-rearing, or they are polylectic with *Salix* being at least an important component of their floral visits. The other 20 species do not visit *Salix* blossoms for pollen.

The 20 species which do not use *Salix* either have their ranges split by the prairies (nine species) or are found to occur only in the northern reaches of prairies (11 species) across Manitoba, Saskatchewan and North Dakota (Table 2). Of the 24 species which do use *Salix* pollen, 18 range across the prairies south of North Dakota as well as across the north (Table 3). The remaining six species are exceptional in that they do visit *Salix* catkins but have their ranges split by the prairies.

In general, North American *Andrena* which are wide-spread and vernal do not cross the western Great Plains south of North Dakota unless *Salix* is a strong component of their floral preferences. Of the six species (Table 3) which are exceptions to this rule, the first (*A. wellesleyana* (Robertson)) is a *Salix* oligolege but is rare in collections and may prove to occur in the more southern plains region. Two species (*A. algida* Smith and *A. rufosignata* Cockerell) seem to be polylectic bees, and *Salix* may prove to be a minor source of pollen for these species when more information becomes available. The remaining three species, *A. sigmundi* Cockerell, *A. clarkella* Kirby and *A. frigida* Smith, are oligoleges of *Salix* and valid exceptions to the rule. In any case, all six species are cold-adapted early spring species, which may be sufficient reason for their absence farther south in the prairies.

In summary, most of the *Salix*-visiting *Andrena*, such as *A. erythrogaster* (Ashmead) and *A. subaustralis* Cockerell, may have had their ranges affected and, perhaps, split by the glaciers during Pleistocene times. Fig. 1 summarizes these data. However, the interglacial periods with expanded prairies probably affected the distribution of non-*Salix* bees in the same way, whereas the glacial periods allowed the migration of these species from east to west and vice versa.

Seventeen other transcontinental species of *Andrena*, all oligolectic, were found to occur commonly in the prairies south of North Dakota (Table 4). Two of these, *A. geranii* Robertson and *A. violae* Robertson, are vernal or early summer bees. The remaining species are summer or fall bees and are oligolectic on such plants as *Geranium, Rhus, Amorpha*, and several Compositae. These summer floral specialists are able to survive and occur throughout the central and southern prairie region.

From such considerations, it appears that the availability of food plants, in conjunction with other ecological factors, affects the distribution of at least some species of *Andrena*, even though the

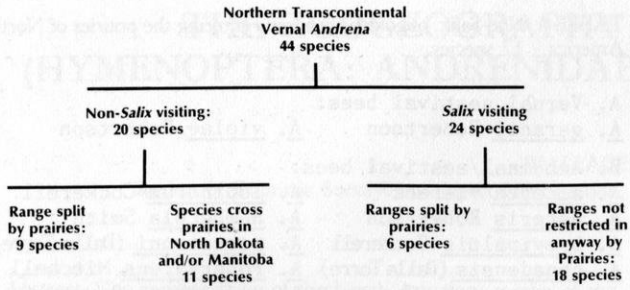

FIG. 1. The distribution of transcontinental species of Andrena with respects to the Great Plains and Salix.

species are not oligolectic. Also, it is possible that the interglacial period restricted gene-flow between populations of some species (polylectic, non-*Salix*, vernal species) while the glacial periods could have restricted gene-flow between populations of other species (oligolectic on *Salix*, or *Salix*-visiting and polylectic, vernal species). This dynamic situation provides a partial explanation for the large number of species in this genus in North America.

PHYLOGENY AND INTERCONTINENTAL MIGRATIONS

The *Andrena* of the Western Hemisphere are grouped into 50 subgenera, 13 of which are also found in the Eastern Hemisphere which has an additional 37 subgenera. A total of 87 subgenera are now known, but a few are yet to be described, especially from North America. Several primitive subgenera are found in both Hemispheres, although North America seems to have more primitive subgenera than does Eurasia.

Among the most primitive of living subgenera of *Andrena* are the subgenera *Andrena, Notandrena, Gonandrena* and their relatives (LaBerge and Ribble 1972, LaBerge 1980). The ancestor of *Andrena* was probably a species similar to *Andrena* s. str. in having the moderately long malar space and the well-formed pronotal angles and carinae, but more like *Notandrena* in the tergal vestiture, punctation and male clypeus and mandibles. There exist today a few species of *Andrena* in North America - *A. banksi* Malloch, for example - unplaced as to subgenus, which may represent the most primitive *Andrena*. Eurasian species in this group may also exist, but are unknown to the author at present.

Ancestors of *Andrena* s. str. probably gave rise to the *Cnemidandrena* at a time when these bees could freely pass between the two hemispheres, perhaps in Paleocene or Eocene times. It is presumed that *Andrena* s. str., *Cnemidandrena* and the *Gonandrena-Notandrena* lines were all present on the North American continent and in Eurasia at the time these land masses separated. This separation in early to middle Eocene (McKenna 1972) need have been only moderate in order to prevent crossing from one land mass to the other, as *Andrena* seem not to be able to cross even moderate oceanic stretches.

In North America the *Notandrena* line gave rise early to a specialized form now found in the west, the subgenus *Geissandrena*, and to the *Gonandrena* - both of which remain endemic to the Nearctic. The Holarctic *Cnemidandrena* flourished especially in North America where a large number of species associated with drier western habitats exist today (Donovan 1977). In Eurasia the *Cnemidandrena* are relatively poorly represented, and a few species seem to be closely related to North American species, perhaps being Pleistocene sister species of Nearctic forms. The Pleistocene migration of *Cnemidandrena* seemingly was largely or entirely west to east.

The *Cnemidandrena* represent what was, perhaps, the earliest shift of *Andrena* from forest-related plants of the Holarctic Region to the plant family Compositae. These bees have become specialists on flowers of the tribe Asteriae (*Aster, Solidago, Chrysothamnus*, etc.) and the Nearctic group evolved a single, highly specialized species (*A. mentzeliae* Cockerell) restricted to the plant genus *Mentzelia* of the family Loasaceae. This shift in floral preferences also involved a shift in seasonality associated with host shifts from predominantly spring and early summer flowering forest forbs, trees and shrubs (visited by the *Notandrena* and *Andrena* s. str.) to summer and fall-flowering plants of forest and prairie (visited by the *Cnemidandrena*). The bees must also have become more heat tolerant, which has allowed them to range farther south into Central Mexico where *Cnemidandrena* is represented by several endemic species. A sister subgenus, the cold-adapted *Gonandrena*, on the other hand, remains associated with the eastern forests or the western mountains and its species are rare or absent in the central plains as far south as Mexico.

It is hypothesized here that the *Leucandrena*, another early offshoot from the *Notandrena* stem, was distributed on both continents when the continents were separated. The North American *Leucandrena* gave rise to the *Larandrena* and its derivatives, *Parandrena* and *Pelicandrena* (LaBerge and Ribble 1972). The Nearctic *Parandrena*, being cold-adapted *Salix* dependent bees, were able to range farther north than most *Gonandrena* and were able to range throughout the American Great Plains as well. One species of *Larandrena* found in Japan, *A. yatsumatsui* Hirashima, represents an annectent form between true *Larandrena* and *Parandrena*. *Andrena miserabilis* Cresson, the sole Nearctic representative of *Larandrena*, is very little different from the Palearctic *A. ventralis* Imhoff and probably represents a Pleistocene migration across the Bering land bridge.

The *Tylandrena* line probably arose in North America from a primitive species of *Andrena* s. str. (LaBerge and Bouseman 1970). No Old World representatives of this subgenus are known today. Three species of *Tylandrena* cross the Great Plains in North America, *A. erythrogaster* (Ashmead), *A. perplexa* Smith and *A. wilmattae* Cockerell. Only *A. erythrogaster* is abundant in the prairies and it frequently visits *Salix* catkins. Both *A. perplexa* and *A. wilmattae* have ranges which appear to be interrupted by the central Great Plains and neither species visits *Salix*.

The exclusively Nearctic subgenus *Callandrena*, including 80 species, is a second line of *Andrena* which has become warm-adapted, more or less oligolectic on various species of Compositae, especially the tribe Heliantheae. As originally conceived by LaBerge (1967), the phylogeny of this large group of bees involved a single origin from a *Chrysandrena*-like ancestor. In fact, the primitive North American members of *Callandrena* could easily fit into the subgenus *Chrysandrena*, which at present is restricted to the Old World. A large taxometric study of the relationships of the included species was completed by Molina-Pardo (1973). It upholds the cladistic arrangement arrived at by LaBerge in a general way, but lends some credence to the idea of two origins for the *Callandrena*. If this proves to be reasonable after additional study, 25 species now in *Callandrena* will be separated into a new subgenus.

In either case, the shift from cold-adapted, forest-related, floral preferences of the *Chrysandrena* to the warm-adapted preference for the Compositae has allowed the *Callandrena* to range farther south than most other *Andrena*, and this subgenus is the only group of *Andrena* with a large number of species in Mexico and Central America. If two subgenera are involved, they are both represented in Mexico and show the effect of having evolved away from a dependence upon flora associated with the forests and forest margins of more northern climes. Also, if two subgenera are recognized, it will be necessary to hypothesize a considerable degree of *Charitandrena* and *Callandrena*. These convergences involve mouthparts and pollen-collecting hairs, both of which could be related to preferences for composite pollens which these subgenera all exhibit.

Another group of subgenera for which a reasonable cladistic hypothesis is available is the *Trachandrena-Scrapteropsis-Biareolina-Rhaphandrena-Xiphandrena-Onagrandrena* group. Of

these, the subgenera *Rhaphandrena* and *Xiphandrena* seem to be the most primitive and are, perhaps, derivatives from an ancestor not far removed from the primitive *Andrena* s. str.-*Notandrena* stem discussed above (LaBerge 1971). *Rhaphandrena* includes three southwestern vernal species dependent upon cruciferous pollen (especially *Lesquerella* spp.). *Xiphandrena* is a monotypic subgenus and the included species, *A. mendica* Mitchell, is a rare eastern species which flies in late spring. Neither *Xiphandrena* nor *Rhaphandrena* are known in the Old World.

Another subgenus, perhaps related to the *Rhaphandrena*, which arose in association with *Oenothera* in the American southwest, is the subgenus *Onagrandrena* (Linsley and MacSwain 1955, Linsley, MacSwain, Raven and Thorp 1973). These interesting black *Andrena* appear to avoid the extremes of heat of the desert regions by visiting plants only in the early morning when pollen is available. About 24 species, some with recognizable geographic races, have evolved, all associated with *Oenothera* or its relatives *Anogra, Clarkia* and *Camissonia*.

The western subgenus *Diandrena* which occurs in the Rocky Mountains to the West Coast is a possible derivative of the *Rhaphandrena-Xiphandrena* line. It includes 25, mostly oligolectic, species and was revised by Thorp (1969).

Scrapteropsis is a large subgenus consisting entirely of vernal bees associated with spring flowering forbs, shrubs and trees of forests and forest margins and is restricted to North America. Most species are rare in the Great Plains unless *Salix* is a strong component of their polylectic floral preferences (as is the case for *A. imitatrix* Cresson). One species, *A. alleghaniensis* Viereck, occurs in the northeast and in the Rocky Mountains of Utah and Colorado. It apparently does not occur in the Great Plains but ranges to the mountains across southern Manitoba and Saskatchewan. A group of six related species (the *stipator* group) occurs only in the Pacific Coast states. This group was an early off-shoot of *Scrapteropsis* and, although little is known concerning their floral preferences, they seem to be important visitors to *Platystemon californicus* Bentham (Papaveraceae). Two species (*A. daeckei* Viereck and *A. kalmiae* Atwood) from the northeast are oligoleges of Ericaceae, especially the mountain laural *Kalmia* sp.

One line of *Scrapteropsis* must have crossed the Bering land bridge at an early date or was isolated in Eurasia at the time of the continental shifting in early to middle Eocene. This line has evolved into the monotypic Eurasian subgenus *Biareolina*, a distinctive form closely related to *Scrapteropsis*. The subgenus *Brachyandrena* also represents the *Scrapteropsis* in Eurasia, but few species are known to the author.

Another derivative of the *Scrapteropsis* is the large subgenus *Trachandrena* (LaBerge 1973). This group includes 24 Nearctic species and one common Palearctic species, *A. haemorrhoa* (Fabricius). The *Trachandrena* probably arose from a *Scrapteropsis* ancestor similar to *A. ilicis* Mitchell. The single Eurasian representative probably represents another relatively recent, migration from west to east across the Bering land bridge of Pleistocene times. The closest Nearctic relative of the Eurasian *A. haemorrhoa* (Fabricius) is *A. hippotes* Robertson, a transcontinental species that ranges relatively far to the north in western Canada.

As in the *Gonandrena* and *Scrapteropsis*, most *Trachandrena* are vernal species associated with flowering forbs, shrubs or trees of forests or forest margins. Species abundant on the Great Plains (such as *A. hippotes* Robertson, *A. mariae* Robertson, *A. forbesii* Robertson) all have *Salix* spp. as a strong component of their floral preferences, although all are polylectic. Those that do not use *Salix* extensively (e.g., *A. miranda* Smith) are either restricted to the northeast or to the western states or cross the plains only in the northern areas of southern Manitoba and North Dakota. One specialized species restricted to the prairies, *A. quintilis* Robertson, is an oligolege of leadplant (*Amorpha* sp.).

The *Euandrena-Thysandrena* line of *Andrena* probably evolved from a *Rhacandrena*-like ancestor (LaBerge and Ribble 1975, LaBerge 1977). The subgenus *Rhacandrena* includes four North American species. Whether or not it is present in Eurasia is not known at this time. The *Rhacandrena*, although primitive for this line of bees, is a relatively specialized subgenus with each species oligolectic on a few species of plants (three species on *Rhus* and one on *Amorpha*). These plant preferences, like those of *Cnemidandrena* and *Callandrena*, have allowed these bees to be successful on the prairies during late spring and summer months. Although *Rhacandrena* are morphologically near the ancestral stem of the group, they are probably not directly ancestral.

From a *Rhacandrena*-like ancestor several lines radiated. One line produced a large number of Old World and New World species in several subgenera (*Simandrena, Micrandrena, Scaphandrena*). Since so many Old World species are involved (well over 100) and so few are known to the author, details of their evolution and zoogeography will not be discussed here.

A relatively early line from the *Rhacandrena*-like ancestral form was the subgenus *Euandrena* which is abundantly represented in both the Old World (20 species or more) and the New World (25 species). Specializations have occurred in both areas leading to the recognition of specialized subgenera (*Thysandrena, Dasyandrena* and *Psammandrena* in North America). It is of interest that *A. hebes* Perez, known only from Japan, is almost indistinguishable from our Nearctic *A. nigrihirta*(Ashmead), and that the Eurasian *A. ruficrus* Nylander is closely related to the North American *A. algida* Smith. Since both *A. nigrihirta* and *A. algida* today range north to or almost to the Arctic Circle, it seems likely that they are either relatively new members of the Nearctic fauna or that their sister species (*A. hebes* and *A. ruficrus*) represent Pleistocene migrations to the Palearctic region. Both *A. nigrihirta* and *A. algida* are polylectic, cold-adapted, vernal bees associated with forbs and shrubs of forest and tundra. *Andrena algida* seems to be an exception among the Neartic *Andrena* which are widespread and polylectic in that it does not occur in the Great Plains area (except in the north) in spite of its predilection towards *Salix* blooms. *Andrena nigrihirta* has roughly the same pattern of distribution as *A. algida* but is not known to visit *Salix*.

The subgenus *Thysandrena* probably arose from a *Euandrena* ancestor in North America. Eurasia has few species of *Thysandrena* and they have not been available for study. Perhaps they represent a Pleistocene migration into Asia from North America. The Nearctic *Thysandrena* have evolved highly specialized western forms (*Dasyandrena* and *Psammandrena*) and, although several species are *Salix* visitors, only one has a transcontinental distribution (*A. w-scripta* Viereck). The only other eastern representative of *Thysandrena* (*A. bisalicis* Viereck) is a *Salix* oligolege which does occur in the central Great Plains of Illinois, Iowa, and Nebraska. Both *A. algida* and *A. w-scripta* in the eastern part of their ranges appear to be associated with the boreal forests and do not range far to the south. Perhaps they are exceptions to the *Salix* rule of the Great Plains because they are more cold-adapted than most *Andrena*, or they may both have extended their ranges to the east only in recent times, since the last Pleistocene glaciation.

The *Melandrena* are abundant in both Eurasia and in North America. The author considers them to have derived from a *Euandrena*-like ancestor and to be of North American origin (Bouseman and LaBerge 1979). At least all of the Palearctic species studied thus far belong to the more advanced group of *Melandrena*. The primitive group is found only in the Nearctic region. The subgenus *Melandrena* is convergent with *Tylandrena* in a number of characteristics. Both subgenera include relatively large bees that have unbanded terga, rather large-heads, and long mandibles in the males. The *Melandrena* also include a number of transcontinental, polylectic, vernal species (*A. regularis* Malloch, *A. carlini* Cockerell, *A. vicina* Smith, *A. commoda* Smith, *A. nivalis* Smith). Of these, only *A. commoda* and *A. vicina* are common in the Great Plains south of northern North Dakota. Both species visit *Salix* flowers.

CONCLUSIONS

The genus *Andrena* is primarily Holarctic in distribution with few extensions into Africa south of the Sahara, India, southeast Asia and Central America.

Moderate oceanic stretches present important barriers to migration of *Andrena* species.

Plant sources of pollen for brood-rearing have important effects on the distribution *Andrena*. Oligolectic species restricted to one or a few related pollen sources may be more or less restricted in range by the range of the host plant(s).

Edaphic factors may affect distribution of *Andrena* species if they are restricted to a particular substrate for nesting.

In North America many transcontinental species of *Andrena* seem to be absent from or rare in the Great Plains area, although they may cross the prairies in the far north (southern Manitoba and Saskatchewan and North Dakota). All vernal *Andrena* species that cross the plains in abundance and are not restricted to the northern area of the prairies (18 species) have *Salix* spp. as an important component of their pollen sources. A few species which utilize *Salix* but do not enter the Great Plains south of North Dakota, form exceptions to this rule (six species).

Pleistocene glaciations isolated populations of *Andrena* species (eastern and western populations). The food plant preferences had an effect upon this isolation, in some cases reinforcing it. Transcontinental species of *Andrena* not using *Salix* as an important pollen source were pushed to the southeast and into mesic habitats in the Rocky Mountains by the glacial intrusions. Morphological change occurred in some of these isolated populations to the extent of producing distinct species.

At least two periods of land connections allowing *Andrena* migrations between the Palearctic and the Nearctic regions would explain the seemingly ancient and the more modern exchanges of fauna which seemingly occurred between these continental masses. The appearance and then disappearance of a single Pleistocene Bering land bridge and the connection or near connection of North America and Europe during the middle Eocene (or earlier) can account for the evolutionary divergences in *Andrena* discussed above. No other land connections need be postulated, but this does not preclude several Bering land bridges during late Pliocene or Pleistocene times.

An evolutionary shift from vernal to summer or fall activity occurred independently in at least four lines of *Andrena* (subgenera *Cnemidandrena, Callandrena, Plastandrena* and *Rhacandrena*). The *Rhacandrena* change involved specializations on *Rhus* (Anacardiaceae) and *Amorpha* (Leguminosae) and the remaining three involved Compositae in part. All four involved shifts from cold to heat tolerant behavior and the first three subgenera evolved important faunas in Mexico and Central America.

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Part 5. INTERFACES BETWEEN GRASSLANDS AND WOODLANDS

EVIDENCE OF THE HISTORICAL OCCURRENCE OF WOODY PLANTS IN AREAS OF NORTH DAKOTA GRASSLANDS

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Abstract. A paucity of woody plants has been the common assumption about presettlement grasslands in North Dakota and nearby areas. However, there is contradictory evidence from both direct and indirect sources. Direct sources include oral and written statements from pioneer citizens and written reports of plant material use by native American Indians. Indirect sources include data and field observations from studies of prairie fires during the past 16 years. Records of environmental conditions prevalent during historic times (climate, topography [including wetlands], prairie fires, animal digging, actions of native ungulates) were also inferential sources.

I conclude that conditions and mechanisms present during historical times were adequate to help maintain woody plants in small local areas and in some large areas of the North Dakota grasslands.

INTRODUCTION

Excepting for riparian woodlands and a few areas of oak-savanna, it has long been assumed that the presettlement grasslands in North Dakota and nearby areas were mostly or entirely devoid of woody plants, particularly trees and tall shrubs. Even early visitors like Catlin and Maximilian referred to the area as uniformly sterile or as desert. Further, some grassland ecologists support the theme that "there were no trees or shrubs." The objective of this paper is to present some historical evidence that clarifies the occurrence of woody plants in northern grasslands.

REPORTS OF SCARCE WOODY VEGETATION

The following historical accounts support the contention that woody plants were absent or nearly so in northern grasslands. In the Dakotas during June 1810, Bradbury (1966:149) wrote: "The whole of the plain (central North Dakota) was perfectly level, and like the rest of the country without a single shrub." About 1835, Catlin (1965 II:171) described the prairie coteau in eastern South Dakota: "There is not a tree or bush to be seen from the highest summit of the ridge ...."

Harmon (1922:81) stated that in 1804 near Alexandria, Manitoba, "Not a tree could be seen, as far as the eye could extend." Similarly, Alexander Henry and Thompson (1965:308) reported that in 1806 near the Moose Mountains in southeastern Saskatchewan the "Riviere la Souris, thus far up, is but thinly wooded; at some places there is none at all for several miles. The land on each side is high, and stretches out into the level prairie, as far as the eye can reach no wood is to be seen in any direction." Palliser (1968:112) referred in 1857 to the area south of what is presently Winnipeg, Manitoba. He stated, "There is not a vestige of wood, so we are again dependent on buffalo dung for fuel."

Macoun (1882:27) found "That part of the prairie lying west of Moose Mountain, and a line connecting it with Touchwood Hills, may be said to be wholly without wood between the Boundary and lat. 52° north. Wood Mountain and the Cypress Hills together with narrow river valleys are the only exceptions." Henry Yule Hind (1969) in 1858 reported (p. 338), "Wood began to be a great treasure in the prairie after passing the Moose Jaw Forks .... No tree or shrub or even a willow twig could be seen in any direction ....;" (p. 306) "Our half-breeds informed us that this great prairie west of the Souris (River) continues treeless and arid for a distance of sixty miles ...."

REPORTS ON THE PRESENCE OF WOODY VEGETATION

Prior to 1914, Melvin Gilmore interviewed native American Indians to find out what plants they used. According to Gilmore (1977), cottonwood (*Populus deltoides*) Marsh, willow (*Salix* spp.), ash (*Fraxinus pennsylvanica*) Marsh, chokecherry (*Prunus virginiana*) L., and Juneberry (*Amelanchier alnifolia*) Nutt. were the principal woody plants used by the northern plains Indians. Cottonwood and willow were used for lodge construction and firewood, ash for bows, Juneberry for arrow shafts, and Juneberries and chokecherries as food items and for use in making pemmican. These woody plants still exist in limited amounts on untilled prairie areas throughout much of North Dakota, but only in isolated areas where soil and moisture conditions are conducive to woody plant growth.

In one of our earliest historical accounts, La Verendrye (1927:318) reported in 1738 in the area between the Souris River and Mandan villages, "They often make their dogs carry firewood even as they frequently have to camp in mid-prairie, the clumps

of trees only occurring at distant intervals.''

Phillip de Trobriand (1951:322) in 1868 recounted, ''Dog Den (central North Dakota) ... is a collection of rather abrupt hills, separated by deep ravines well covered with trees, ...'' In an 1806 description of the area between the Missouri and Souris rivers in North Dakota, Henry and Thompson (1965:405) stated, ''At five o'clock we came to a small lake on which grew brushwood and poiriers (pear trees literally, but here meaning Juneberry shrubs) whose branches were loaded with fruit; ....'' Larocque (1934:14(4):334), while traveling in the Badlands area of western North Dakota in 1805, wrote, ''... we arrived at noon on the banks of the Little Missouri .... A few sparse cotton-woods grow here and there on the edges ... the plains are made up of rock of which the summit and the sides are partially covered with red pine and with some other varieties of wood, such as poplar, elm, ash, and a kind of maple.''

Dodge (1965:144), in a western South Dakota expedition in 1875, wrote ''... from Camp Robinson to the Cheyenne is through 'badlands' ... grass is generally poor, and wood almost entirely lacking.'' Christy (1892:98) wrote, ''These sand-hills, ... are usually sparsely covered with stunted timber trees.''

Theodore Roosevelt (1885:2) reported, ''The Northern cattle plains occupy the basin of the Upper Missouri; .... The character of this rolling, broken, plains country is very much the same. It is a high, nearly treeless region, of light rainfall ....''

Joseph Nicollet (1976:185) recounted, ''At 8:00 we cross the Sheyenne River (near present Hamar, North Dakota, in Eddy County in 1839), ... Woods of oak, white elm, white ash, and a variety of berry bushes, all scarce in these faraway lands.'' He also wrote that at a distance of ''Four miles along our route after leaving the Sheyenne (River) we have passed near a woods formed entirely of aspen and lined with wild plum trees and berry bushes.'' John Tanner (1975:50) reported that in the late 1700's, ''The place to which we went on the Assinnebain, is seventy miles distant by land from the mouth; .... The banks of the river, on both sides, are covered with poplar and white oak, and some other trees, which grow to considerable size.''

Christy (1892:98) noted, ''Another fact, familiar to everyone that knows the prairies ... is that nearly all the streams crossing the prairies are fringed with a narrow belt of trees on both sides, ... This is the case even on absolutely treeless prairies, on which grass will scarcely grow, ...''

The descriptions by Catlin and Bradbury of treeless plains also mention woody plants. Catlin (1965 I:72-73) in 1835 stated that ''... in every direction, there were little copses and clusters of plum trees, gooseberries, and wild currents loaded with their fruit, ... and ... the wild rose bushes ....'' Bradbury (1966:158) in 1810 reported, ''... of which abound (west of present Mandan, North Dakota) a new species of *eleagnus*, intermixed with a singular procumbent species of cedar (*juniperus*). The branches are entirely prostrate on the ground, ...''

Another traveler, Nicollet (1976:86), wrote in 1838 from Lincoln County, Minnesota, just east of Brookings County, South Dakota, ''This part of the Coteau Perce .... The sides of the ravines are covered with wood that the fire of the prairies and the hand of the Indian have not yet destroyed.'' In another passage (p. 204), he described in 1839 how they ''Arrived at the first eastern coteau (near present-day Veblen, South Dakota) where there unfolds a plain bejeweled with lakes and dotted with beautiful stands of trees.''

Palliser (1968:139) wrote in 1857, ''The Creek before where the Bones lie (about 5 miles north of present Regina, Saskatchewan), ... here we found water and some little grass, also a few willows and cherry bushes, but no wood fit for fuel.''

Hind (1969:294) stated in 1857, ''The prairie on the west of the Souris as well as on the east is treeless, but the bank of Plum Creek support a thin belt of small forest trees, such as oak and ash, with a few ash-leaved maple.''

John Macoun, a field naturalist and botanist for the Canadian government explorations, gave this descriptive account in 1882 (p. 102): ''This tract of bad land is principally combined to the section between the 111th and 112th meridians and between the 51st and 52nd parallels. This extensive tract is almost wholly without wood of any description. Not a shrub enlivens its surface except occasional clumps of rose bushes (*Rosa blanda*) a few inches high, the western snowberry (*Symphoricarpus occidentalis*), and the beautiful silverberry (*Eleagnus argentea*). These could not be called bushes except on the ground of being woody. They are never seen more than three years old and hardly ever that.'' He further wrote (p.191-192), ''After passing out on to the 'Souris Plain' .... One hundred miles and upwards are crossed and the only shrubs seen are the two snowberries (*Symphoricarpus racemosa et occidentalis*) and the rose bushes ....'' He also reported, ''The Turtle and Moose Mountains, Brandon Hills, Pheasant Hills, File Hills, Touchwood Hills, and other small groups ... are in most cases merely a series of ridges and rounded drift eminences encompassed by marshes and lakelets, which prevent the destruction of their forests from fire at uncertain intervals. Therefore, the wood on them ranges from mere twigs of a year old, up to trees eighteen inches in diameter.''

PROTECTION OF WOODY PLANTS FROM FIRE

Some historical accounts relate wetlands, swamps, and potholes with woody plants in the northern grasslands. Nicollet (1976:260-267) reported that near Spring Lake in Day County, South Dakota, in 1839, ''The prairies are without wood, frequently swampy, and we are forced to accept a little lake whose shores are covered with brush.'' In 1883, Christy (1885:123) wrote that the area 105 miles west of present-day Winnipeg, Manitoba, had ''In the moister parts, where lakes and ponds arrest the progress of the fires, extensive woods of poplar ....'' He later reported (1892:80) on the true prairie region of Manitoba and the Dakotas: ''In speaking of the tree-lessness of the prairies, I of course do not forget that, even in many truly prairie areas, the swampy parts and islands in lakes are often timbered, while belts of trees fringe most of the streams, ...'' Gleason (1912:48) wrote about the prairies of Illinois in 1912: ''In this way it becomes evident that, in every case, those ridges which are or were forested are protected from prairie fires on the west by a conspicuous slough ....''

''Fire shadows'' on the leeward side of wetlands offer a condition whereby woody plants can escape the effects of prairie fires. Recent evidence of the relationship of wetlands, fire shadows, and presence of woody plants in the prairies came from personal interviews with S.J. Larson, Courtenay, North Dakota, and R. Cook, Woodworth, North Dakota. Prior to 1931, S.J. Larson and his brother found 160-640 acres of unburned prairie on the southeast side of the Northwest Lakes in Roosevelt Township of Stutsman County during an early fall hunt. It had many sharp-tailed grouse concentrated in the brush which was surrounded by recently burned prairie.

During 1909-1912, Ruth (Wingire) Cook lived about 9 miles northeast of the present townsite of Woodworth. She said chokecherry and thornapple shrubs (*Crataegus* spp.) were plentiful, as were applebrush (silverberry [*Eleagnus commutata*]) and badger bush (buckbrush [*Symphoricarpos occidentalis*]). They used chokecherry bushes for Christmas trees and the taller silverberry brush for whips. She described a prairie fire in about 1911 that burned much of the area except for a large portion on the north side of the Northwest Lakes which included her parents' farm. Thus S.J. Larson's and R. Cook's accounts have shown how one set of prairie lakes produced two fire shadows, one north and one south.

Further, the following personal observations identify some conditions whereby native woody plants were able to survive recent prairie fires on or near the Woodworth Field Station of the Northern Prairie Wildlife Research Center. Frequently burned sites exist on the Woodworth Station where we have one fire demonstration plot which has been ungrazed but burned 12 of

the past 18 years (1967-1984). Fires were ignited during April, May, or June, except in 1972 when the plot was burned on July 31. This plot still supports a fair population of buckbrush, silverberry, wild prairie rose (*Rosa arkansana*), and one small clump of chokecherry, although it is much reduced in height and density. Thus, this plot demonstrated that at least four species of native shrubs were able to survive a high frequency of fires.

Woody plants were not affected by prairie fires where fine ground fuels were absent because of bare soil conditions resulting from ungulate trampling, rubbing, and wallowing or from soil depositions resulting from wind and water erosion or burrowing mammals. The woody plants growing on dirt mounds at two badger (*Taxidea taxus*) dens were not burned during six prairie fires. During spring, woody plants were occasionally protected from prairie fires by snowdrifts. On the prairies and plains, snowdrifts are larger and deeper near patches of woody plants, in ravines or behind embankments. The taller and deeper snowdrifts are the last ones to melt and provide fire protection to woody plants until the snow is entirely gone. Thus, large areas of grassland can be burned without affecting woody plants protected by snowbanks.

Wetlands potentially provide three sources of fire protection to woody plants. Islands within wetlands are protected from fire and more often than not have stands of woody plants including trees. Moist soil conditions of wetlands also provide fire protection and prime sites for woody plant growth, particularly for willows, cottonwoods, and poplars. Further, small wetlands can have "fire shadow" areas on their leeward sides just like the fire shadows that occur leeward to larger lakes in northern forests.

Woody plants also provide some conditions and mechanisms that insure their own future maintenance within a fire environment. Nearly all of the native species of shrubs, brush, and some tree species reproduce vegetatively by sucker sprouts which arise after fire or grazing protection. In the absence of intensive grazing, dense patches of native shrubs and brush usually produce enough shade to inhibit all but a very sparse undergrowth of grassy-type fuel and often not enough fuel to sustain a fire.

SUMMARY

Quotations from diaries and journals supply evidence for the presence of woody plants. My direct interviews and personal observations describe conditions under which woody plants are maintained in the presence of fire. I have drawn three conclusions: (1) written historical evidence indicates that some trees, brush, and tall shrubs did occur in the interior prairies and plains of North Dakota and nearby areas in the late 1700's (La Vérendrye and Tanner) and into the early 1900's. Thus, some but not a lot of trees, tall shrubs, and brush did exist in the northern prairies during and after the bison era; (2) several authors provided contradictory evidence within the same journal or letter of the presence of woody plants in portions of the northern plains and prairies, other than along streams and rivers. This may suggest that portions of northern grasslands were affected quite differently by fire, weather, grazing, trampling, and American Indians. The referenced accounts suggest that level grasslands contained considerably fewer woody plants than those grasslands with varied topographic relief (Wells 1970) or sandy soils or wetlands. In addition, (3) there is some evidence that trees, tall shrubs, and brush did occur in places other than along rivers, mountains, and hills within the historical grasslands. Written accounts of the treelessness of the prairies are variable due to the obvious subjectivity of some observers; e.g., what was treeless to one person may actually have been scattered shrubs on prairie and trees along a river to another. Also many of these observers came from forested eastern states and perhaps exaggerated their perception of treelessness. Evidence also suggests the total area occupied by woody plants in North Dakota and nearby was small during recent historic times.

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THE EFFECT OF 13 YEARS OF ANNUAL BURNING ON AN ASPEN-PRAIRIE ECOTONE IN NORTHWESTERN MINNESOTA

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Abstract. Studies on the effects of annual and biennial spring burning on prairie rejuvenation and aspen sucker shoot control were initiated in 1971 at the Northwest Agricultural Experiment Station in Minnesota. Plots were back-burned when the new growth of Kentucky bluegrass (*Poa pratensis*) was 10-15 cm high with the goal of suppressing it and favoring warm-season native grasses. After 13 years, in both annual and biennial plots, bluegrass was reduced to about half of the original level, whereas big bluestem (*Andropogon gerardi*) was increased three-fold and little bluestem (*Schizachyrium scoparium*), four-fold. Spring burning was also effective in controlling aspen invasion of prairie with comparable effects noted from biennial and annual burning. Biennial spring burning is recommended over annual burning in prairie management. It yields comparable results, is half the work, and provides residual cover for ground-nesting birds every other year. Preliminary data suggest repeated summer burning may be effective in controlling aspen sucker shoots.

INTRODUCTION

The transition zone between two ecosystems is of interest to ecologists as well as to land managers wishing to understand the controlling factors so they can favor one of the ecosystem types or a combination of both. This paper deals with the use of fire at the Red River Valley Natural History Area (RRVNHA) in Minnesota to maintain aspen parkland, a composite community of aspen (*Populus tremuloides*) groves and prairie located along the continental prairie-forest transition.

This is an update of an earlier paper (Svedarsky and Buckley 1975) and is part of an ongoing study to clarify the effects of fire in prairie management in northwestern Minnesota. The RRVNHA

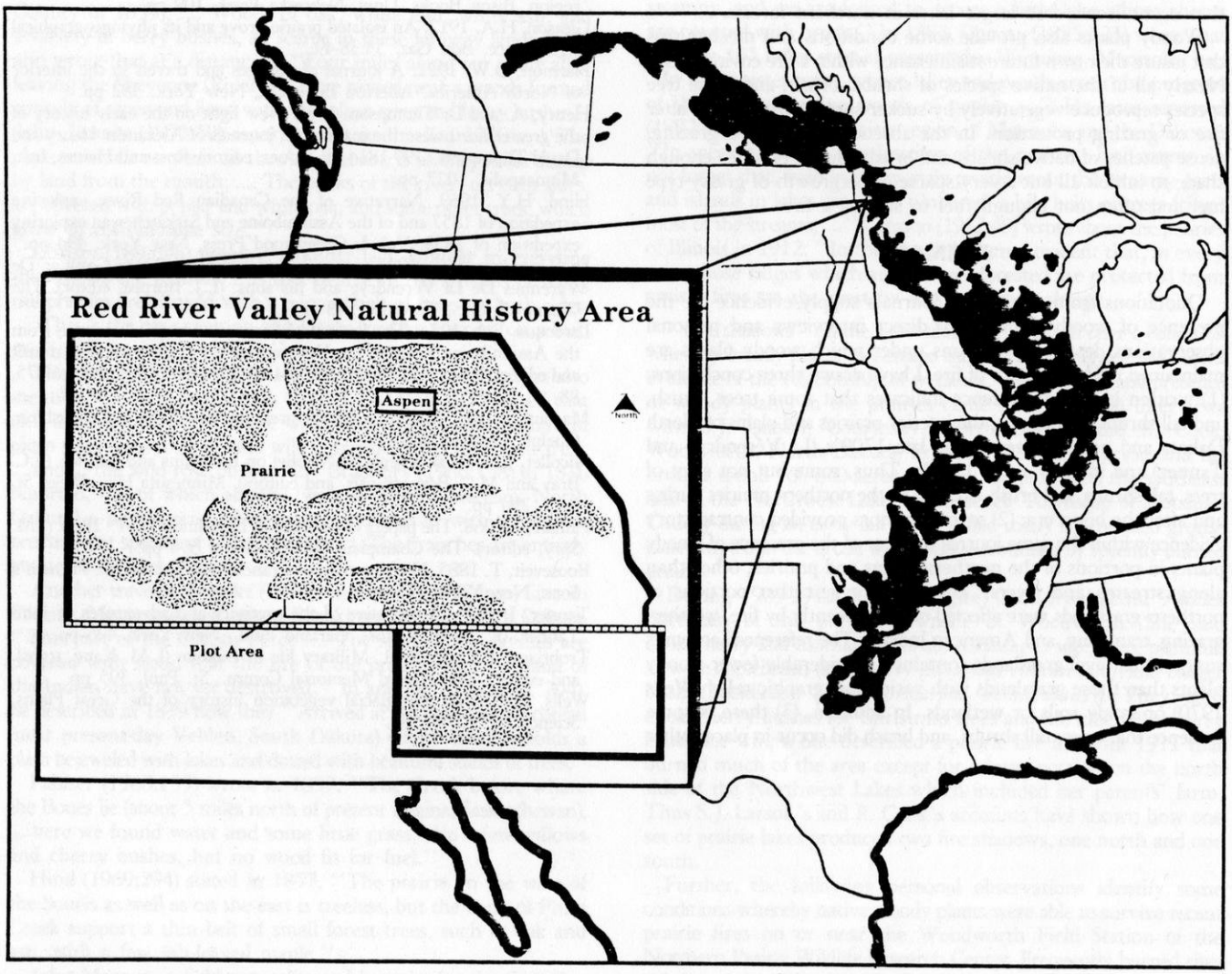

FIG. 1. Location of the study area with respect to the eastern prairie-forest transition area (map adapted from Anderson 1983).

was established as an environmental education and research facility in 1971 after a history of heavy grazing by sheep. Grazing had shifted the vegetative composition of the prairie from warm season native species to cool season exotics, primarily Kentucky bluegrass (*Poa pratensis*). Grazing also had effectively controlled the invasion of prairie by aspen sucker shoots which grew to heights of 0.5-1.5 m the first season after sheep were removed. This paper reports on the effects of 13 years of prescribed burning in: (1) rejuvenating prairie vegetation and (2) controlling aspen sucker shoots in prairie.

STUDY AREA

The RRVNHA is located on the Northwest Agricultural Experiment Station of the University of Minnesota 1.6 km north of Crookston. It is along the eastern edge of the Red River Valley about 16 km west of the prairie-forest transition (Fig. 1). Soils of the Valley are typically fine-grained clay loams but the study area is on an "island" of moderately well-drained, loamy soils developed from calcareous, gravelly sand material (undesignated soils - "Aeric calciaqualls"; Rust and Erickson 1977). The soils in the study area are similar to those along the glacial Lake Agassiz beach ridge complex where the current prairie-forest transition is located. The climate is continental with an average annual temperature of 4.2° C and a range from 13.5° C (average high for July) to -32.7° C (average low for January). The growing season is 125 days; approximately 60% of the 52.5 cm of annual precipitation occurs during that time (Severson 1982). The presettlement vegetation was tallgrass prairie with woody species becoming more prevalent after the elimination of bison (*Bison bison*) and elk (*Cervus elaphus*) and fire suppression (Bird 1961).

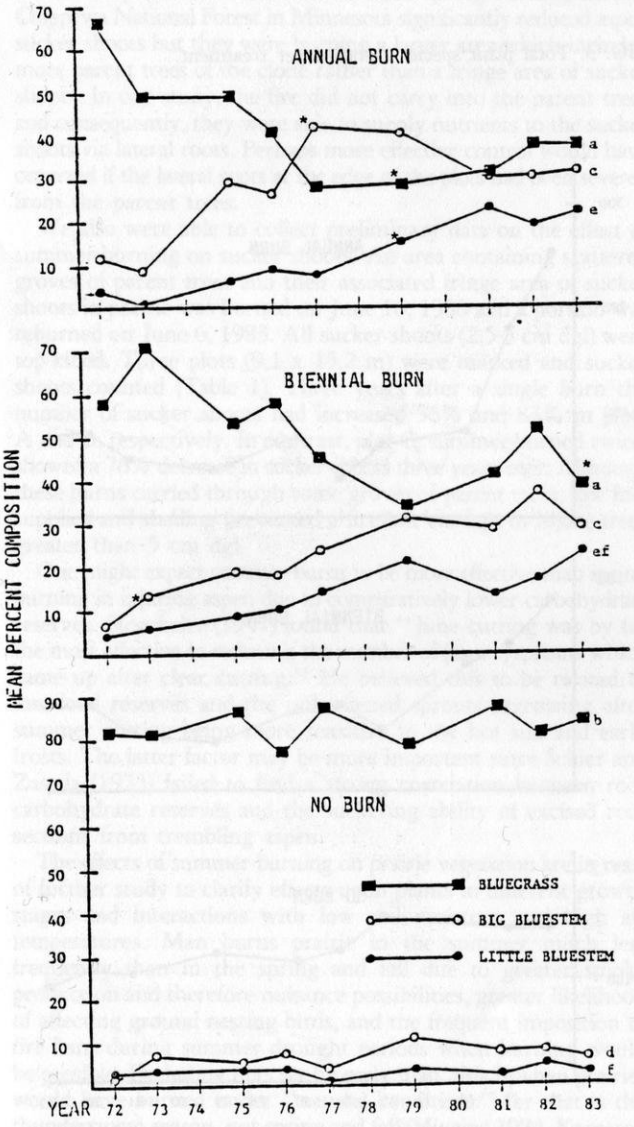

FIG. 2. Effects of spring burning on three grass species. * = the year in which the percent composition for a species within a treatment became significantly different ($P < 0.05$) from 1972, the first observation year (Duncan's Multiple Range Test). In comparing 1983 data for a species, those values followed by the same letter are not significantly different ($P < 0.05$) from other treatments (t-Test).

METHODS

Six plots measuring 18.3 x 7.6 m were established along the south edge of an aspen grove (Fig. 1). All plots had a comparable population of aspen sucker shoots and composition of herbaceous vegetation at the beginning of the study in 1971. Treatments of no-burn control, biennial spring burn, and annual spring burn were randomly assigned with two plots per treatment. Bordering the south edge of the plots is a railroad right-of-way prairie which serves as a seed source of prairie species which can disperse into the plots. Plots were back-burned in late April or early May depending on burning conditions and plant phenology. Because one goal was to injure bluegrass, we tried to burn when its new growth was 10-15 cm high. Herbaceous species composition and basal cover were measured with a 10-point frame (NAS-NRC 1962) in late August or early September. At the same time, aspen sucker shoots were individually counted in a 6 x 7.5 m portion of the plots next to the parent trees in the grove. Plant names follow Gleason and Cronquist (1963) except for little bluestem (*Schizachyrium scoparium*).

RESULTS AND DISCUSSION

Herbaceous Vegetation

After 13 years of spring burning, Kentucky bluegrass was reduced to about half the original percent composition (Fig. 2). Big bluestem (*Andropogon gerardi*) was increased three-fold and little bluestem, four-fold. Big bluestem appeared to respond faster to burning than little bluestem, especially in the annual burn plots. No differences ($P < 0.05$) were observed between annual and biennial burn plots with respect to these three grass species after 13 years. This continued a trend reported in 1974 (Svedarsky and Buckley 1975) and is consistent with early findings of Curtis and Partch (1948). Spring burning suppresses cool-season bluegrass since it is actively growing and drawing upon root reserves at that time. On the other hand, warm-season bluestems are dormant in spring and the increased ground temperatures resulting from litter removal and the dark surface accelerate the onset of growth and buildup of carbohydrate reserves needed for flowering (Curtis and Partch 1950, Henderson et al. 1983). Petersen (1983) suggested that the heat of the fire may have a direct effect by breaking down a heat-labile floral inhibitor in the crown of the plant. Although no temperature data were collected in this study, we observed that fires burned hotter over the years as the vegetation composition shifted from bluegrass to bluestem predominance. Bluegrass tended to mat down more from snow accumulation whereas the bluestem foliage stayed more erect and appeared to allow better drying and inflow of oxygen during burning.

From the 10th year of burning to the present, the proportions of the three reference grass species did not change appreciably (Fig. 2). This suggests that about a 10-year burning period is necessary to rejuvenate a bluestem stand which has been degraded by heavy grazing and/or lack of burning resulting in bluegrass predominance.

The total number of plant species tended to be the highest (5 of 9 years) in biennial burn plots and lowest (7 of 9 years) in no-burn control plots (Fig. 3). Other species which appeared to be

favored by burning in this study were: purple prairie clover (*Petalostemum purpureum*), porcupine grass (*Stipa spartea*), many-flowered aster (*Aster ericoides*), and prairie onion (*Allium stellata*). No significant differences in plant species composition were apparent between annual and biennial burn plots but this may be due to the choice of sampling method; the 10-point frame measures major vegetation characteristics and may not have detected subtle differences. Anderson and Bailey (1980) found, that after 24 years of annual spring burning in the aspen parkland of Alberta, there were generally twice as many species in burned plots as controls. Kucera and Koelling (1964) recommended burning at a two to three-year interval versus annual burning in order to maintain a better species mix. They found annual burning favored prairie grasses and decreased forbs.

The effects of burning are modified by climatic factors preceding and following a fire (Anderson 1983). Plots were burned on April 15 in 1980, a year of an early spring followed by a dry summer with only 8.9 cm of precipitation from January 1 to July 14 accompanied by above average temperatures. This diminished the productivity of the annual burn plots to the extent that there was insufficient fuel to carry a backfire in 1981. This relates to findings in Kansas (Owensby and Smith 1973) where late spring burning favors greater productivity than spring because it reduces the period of soil exposure before the onset of warm-season plant growth. Additionally, burning later in the spring tends to maximize the injury to cool-season species such as Kentucky bluegrass (Henderson et al. 1983).

ASPEN SUCKERS

Background

Trembling aspen is a relatively short-lived (about 40 years) tree with respect to a single stem but it is uniquely adapted to withstand disturbances such as fire and windstorms because it can vigorously produce root sucker shoots when parent trees are top-killed. Aspen grow in clones with hundreds of trees growing from the same root system which produces sucker shoots from lateral roots located sbout 2.5 cm below the surface. Sucker shoot initiation and growth are promoted by a high cytokinin (produced in roots)/ auxin (translocated from crowns) ratio (Schier 1981). Interrupting the auxin source by felling parent trees or destroying the phloem tissue by fire results in sucker shoot production. High root temperatures (24° C is optimum) also promote suckering by stimulating cytokinin production and breaking down auxin coming from the parent tree crown (Perala 1974, Schier 1981). Schier (1976) noted that "high soil temperature in exposed grasslands adjacent to aspen clones is thought to be the primary reason for aspen being able to invade these areas." Trembling aspen in the primary woody species which tends to invade prairies along the prairie-forest transition from West Central Minnesota north to Manitoba, Saskatchewan and Alberta (Bird 1961, Bailey and Wroe 1974, Anderson 1983).

Aspen sucker shoots were reduced by fire in both biennial and annual burn plots, reaching the lowest numbers five to six years after the onset of burning. From 1971 to 1983, sucker shoots declined an average of 62.5% in annual burn plots, 57% in biennial burn plots and 41% in no-burn controls. In 1983, the mean aspen shoot density in the annual burn plots (16,684/ha or 6,752/acre) was not statistically significantly different from biennial burn plots (16,469/ha or 6,665/acre) or the no-burn controls (19,375/ha or 7,841/acre, Fig. 4). Sucker shoots in the control plots were larger than in the burn plots (average diameter at ground level (dgl) = 6.4 cm compared to 1.3 cm) and decreased in number from 1971 due to competitive shading. The shading, which had developed by 1983 in the no-burn controls, was probably affecting the composition of the understory herbaceous vegetation and may have been an additional factor favoring bluegrass over bluestems.

Sucker shoots sprouted within two weeks after burning, presumably in response to the increased temperature caused by

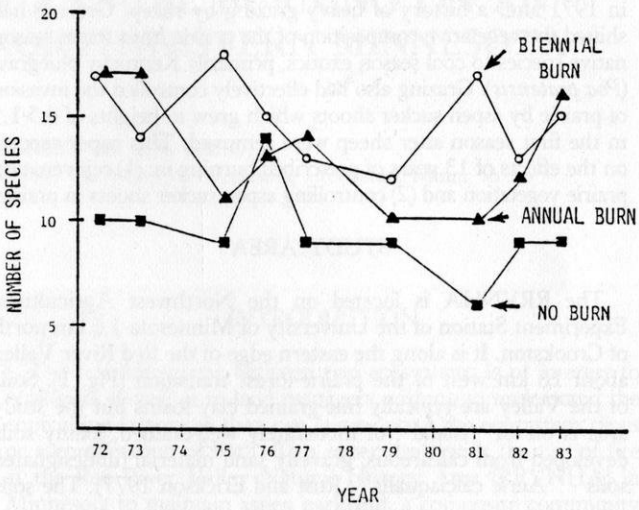

FIG. 3. Total plant species recorded per treatment.

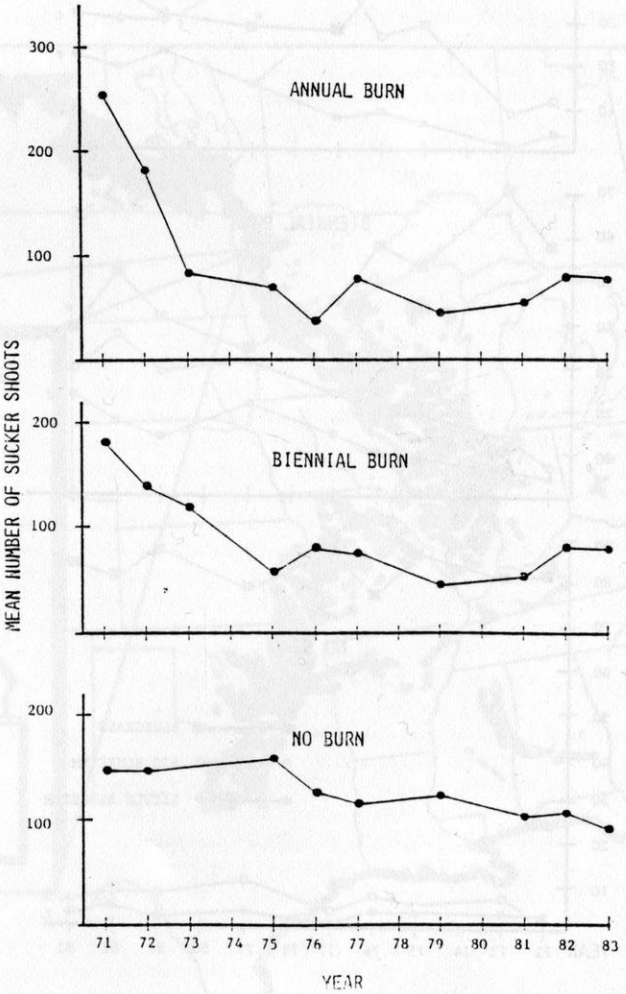

FIG. 4. Effect of spring burning on aspen sucker shoots.

TABLE 1. The effect of summer burning on aspen sucker shoots.[1]

PLOT	NO. OF SUCKER SHOOTS/ha		
	ORIGINAL NO. BEFORE BURN	31 JULY 1980	13 OCT. 1983 and ()=% CHANGE FROM ORIGINAL
A	13,449	10,072	21,014 (+56%)
B	16,739	18,406	30,652 (+83%)
C	11,816	4,203	2,826 (-76%)

[1] All plots burned 16 June 1980; plot C burned again on 6 June 1983. Plots B and C were located within the same clone.

the dark soil surface and by a lack of auxin from the parent trees still developing leaves. Sucker shoots rarely grew more than 1 m high in either the annual or biennial plots and appeared to have no effect on the growth and flowering of prairie plants

Anderson and Bailey (1980) found repeated spring burns in Alberta to check aspen invasion into grasslands although sucker shoot frequency and canopy cover increased. Buckman and Blankenship (1965) found that repeated spring burning on the Chippewa National Forest in Minnesota significantly reduced aspen sucker shoots but they were burning a larger area which included more parent trees of the clone rather than a fringe area of sucker shoots. In our study, the fire did not carry into the parent trees and consequently, they were able to supply nutrients to the sucker shoots via lateral roots. Perhaps more effective control would have occurred if the lateral roots at the edge of the plots had been severed from the parent trees.

We also were able to collect preliminary data on the effect of summer burning on sucker shoots. An area containing scattered groves of parent trees and their associated fringe area of sucker shoots in prairie was burned on June 16, 1980 and a portion was reburned on June 6, 1983. All sucker shoots (2.5-5 cm dgl) were top-killed. Three plots (9.1 x 15.2 m) were marked and sucker shoots counted (Table 1). Three years after a single burn the number of sucker shoots had increased 56% and 83% in plots A and B, respectively. In contrast, plot C, summer-burned twice, showed a 76% decrease in sucker shoots three years later. Although these burns carried through some groves of parent trees, low fuel supplies and shading prevented a fire hot enough to injure trees greater than 5 cm dgl.

One might expect summer burns to be more effective than spring burning in injuring aspen due to comparatively lower carbohydrate reserves. Stoeckeler (1947) found that "June cutting was by far the most effective in reducing the number of (aspen) sprouts which came up after clear cutting." He believed this to be related to low food reserves and the unhardened sprouts regrowing after summer cutting being more sensitive to the hot sun and early frosts. The latter factor may be more important since Schier and Zasada (1973) failed to find a strong correlation between root carbohydrate reserves and the suckering ability of excised root sections from trembling aspen.

The effects of summer burning on prairie vegetation are in need of further study to clarify effects upon plants in different growth stages and interactions with low soil moisture and high air temperatures. Man burns prairie in the summer much less frequently than in the spring and fall due to greater smoke production and therefore nuisance possibilities, greater likelihood of affecting ground nesting birds, and the frequent imposition of fire bans during summer drought periods when burning would be possible. Excluding fires set by early man, this is when prairies would have burned under "natural conditions" for that is the thunderstorm season, not spring and fall (Higgins 1984, Komarek 1965).

SUMMARY

Prescribed spring burning was an effective tool in rejuvenating a degraded prairie and controlling aspen sucker shoot invasion in this study. Biennial burning is recommended over annual burning because: (1) aspen control and stimulation of bluestem grasses is comparable, (2) plant diversity tends to be higher, (3) residual nesting cover is provided every other year, and (4) work is reduced by half. It is unknown whether a burning schedule less frequent than biennial would yield comparable results. A burning period of 9-10 years seems to be necessary to optimize the vigor of bluestem grasses in prairie which has been weakened by grazing and the concomitant shift towards dominance by cool-season Kentucky bluegrass.

Burning in late spring would probably be more desirable than early spring in areas where Kentucky bluegrass and trembling aspen are problems. Both species would have lower carbohydrate reserves later in the season and be more subject to injury. Burning in late spring could be a detriment, however, to some species of ground nesting wildlife and a trade-off would need to be considered. More research is needed to evaluate the effects of summer burning on woody species as well as herbaceous species.

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EASTERN REDCEDAR'S (*JUNIPERUS VIRGINIANA* L.) EXPANDED ROLE IN THE PRAIRIE-FOREST BORDER REGION

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Abstract. During recent research in the 300-year old lead mining region near Dubuque, Iowa, questions were revived about the origin and significance of eastern redcedar. It now forms dense stands on exposed bluffs and ridges and is invading remnant hill prairies in the Upper Mississippi region. A comparison of past and present redcedar distributions was made from historical accounts, early land surveyors' notes, witness accounts and plant community analysis. Eastern redcedar was not abundant by historical accounts and was rarely used as a witness tree. Most of the redcedar population in the Upper Mississippi region is young. Redcedar's expansion into open, fire-protected habitats offers a useful tool for dating and interpreting recent changes in landscapes and land use. Hill prairies in the river bluff areas are disappearing under the shade of eastern redcedar.

INTRODUCTION

Questions about the origins and significance of *Juniperus virginiana* L. (eastern redcedar) which forms dense stands on many exposed bluffs and ridges and is invading remnant hill prairies in the Upper Mississippi region have been revived in the context of recent research on the vegetation of the 300-year old lead mining region near Dubuque, Iowa (Blewett et al. 1983). The focus of the questions has been on how and when eastern redcedar became locally common, and what its presence implies about presettlement and early settlement landscapes.

According to Fowells (1965) eastern redcedar is found in every state east of the 100th meridian (Fig. 1). The broad ecological tolerance of redcedar that is evident from this exceptional range is further illustrated by its presence in conditions ranging from deep alluvial soils to shallow upland soils. The redcedar's intolerance to shade, especially by seedlings, results in typical habitats being shallow upland soils that are too dry for most tree species and abandoned fields that are fire-protected.

Natural reproduction in redcedar is dependent upon seed production, since sprouting or suckering is not known to occur (Fowells 1965). Much of the reproduction occurs from seed falling to the ground, but several bird species including cedar waxwings, robins, starlings and mockingbirds have been observed removing cones from the trees as well as from snow-covered ground (Parker 1951). Others have reported small mammals, quail, grouse, pheasant and turkey consuming the seed and, presumably, aiding in seed dispersal (Fowells 1965).

Drought resistance is a prominent feature of redcedar seedlings which have low leaf surface area combined with deep tap roots. Fire resistance is absent from all stages of development because the thin bark seldom exceeds one-half centimeter in mature stages and is unable to protect the cambium from heat (Arend 1950) even in some cases where the highly flammable foliage fails to ignite.

The maximum age for eastern redcedar is reported to be about 300 years with maximum heights of 30 to 37 meters and diameters in excess of a meter (Preston 1961, Fowells 1965). Rosendahl (1955) cleverly described "well grown" heights on the order of 10 meters and diameters to 0.6 meter. Rosendahl's avoidance of the "mature" description is apropos for the Upper Midwest where few redcedars predate cessation of fires or old fields established after settlement.

METHODS

Historical records, witness tree data, and recent field observations were the primary sources of information available for documentation of the increases in local redcedar populations. Witness trees were tallied from the original land surveyors' notes for Dubuque County, Iowa, and Dane, Grant and Sauk counties of Wisconsin. All of the surveys of these counties were completed during the middle to later 1830's when white settlement first began to take place in significant numbers. On the basis of air photo analysis and field observations that were used to locate present redcedar populations, townships were selected for a thorough review of the surveyors' notes.

Since it could not be assumed that all surveyors were inclined to use redcedar as witness trees, historical notes and individual testimony became important additional sources of information.

A limited community analysis was performed on surveyors' notes from Dubuque County with a modified quarter method described by Cottam (1947) and Cottam and Curtis (1949). The resulting tree composition and density information was compared

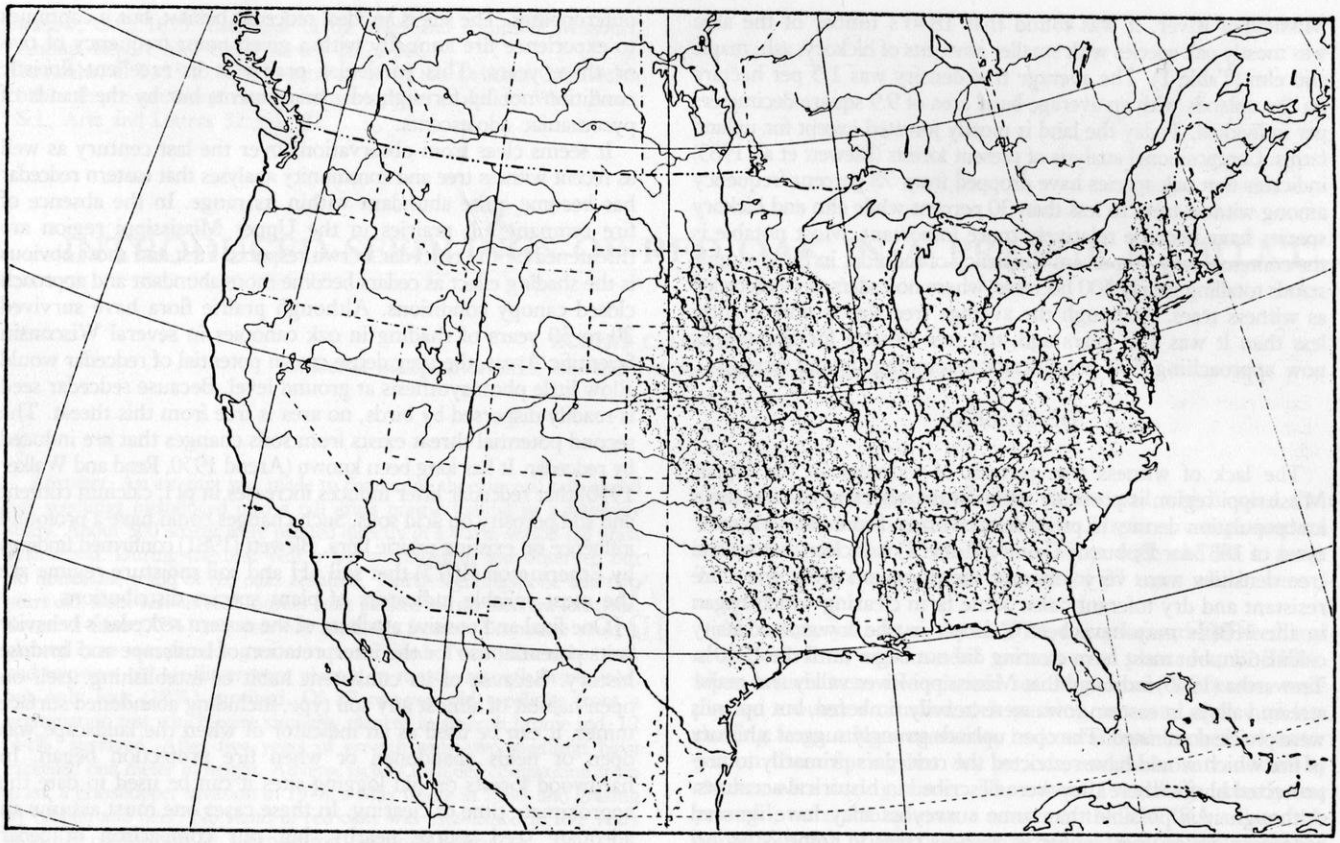

FIG. 1. Distribution of eastern redcedar. Redrawn from Fowells (1965).

with the results of a similar analysis of present day forest in the same area (Blewett et al. 1983).

OBSERVATIONS

Most historical accounts of the 1800's indicate that eastern redcedar was not a common tree, but it could be found along river bluffs, slopes, and bottoms. Arend (1950) reported that in Sharp County, Arkansas, a settler found only 12 redcedars in searching 700 acres in 1854, but today redcedars are plentiful in the same area.

Beilmann and Brenner (1951) review a number of early historical accounts of redcedar in the Ozarks region. Stoddard in 1812 reported redcedar on the Mississippi River extending north of the mouth of the Illinois River. Bradbury in 1819 reported redcedars crowning the tops of some bluffs along the Missouri and Gasconade rivers. Swallow (1855) indicated that redcedar was not common in Missouri, but its habitat seemed to be restricted to dry limestone bluffs. Beilmann and Brenner also reported that before 1900 Franklin County, Missouri, residents had to go east to Jefferson County along the Mississippi to find redcedars, but today it is common into the grasslands of central Missouri in the absence of fire.

Curtis (1959) could not adequately describe the structure of cedar glades in Wisconsin because he and his students (in the 1940's and 1950's) could not find a sufficient number of sites, but Cottam (Personal communication) indicates that many sites that were sparsely populated by redcedars in the 1940's have converted to dense stands in western Dane and Sauk counties of Wisconsin. The Nature Conservancy has had to resort to fire management primarily to save its Spring Green Prairie in Sauk County from being overgrown by redcedar.

Calvin and Bain (1899) reported that some redcedar was being used for fence posts in eastern Iowa, but oak and walnut were the primary sources of fence rail at that time. Today, however, field observations and air photos have been used to show many pure stands of redcedar on hilltops and slopes that would have provided the preferred fence rails in 1900, had they been more plentiful then.

Examination of witness tree data from Dubuque County, Iowa, and Dane, Grant and Sauk counties of Wisconsin has not revealed the use of eastern redcedar as a witness tree in the 1830's. The Wisconsin Commissioner of Public Lands has indicated no recollection of seeing redcedar as a witness tree in any of the surveyors' notes for the state.

On the basis of community analysis of witness trees from a mostly upland portion of Dubuque County adjacent to the

TABLE 1. Witness tree community analysis of Mosalem Township, Dubuque County. Values for relative frequency and relative dominance were calculated from total frequency and total basal area for all species. The importance value (I.V.) is the average of percent frequency and percent dominance.

Species	% F	% DO	I.V.
Acer saccharinum	4.1	2.8	3.5
Carya spp.	8.6	0.7	4.7
Fraxinus spp.	4.1	-	4.1
Juglans nigra	1.9	12.2	7.1
Quercus alba	33.2	52.0	42.6
Quercus macrocarpa	12.3	2.0	7.1
Quercus velutina	33.6	27.1	30.4
Ulmus spp.	2.2	3.3	2.8

Mississippi River, it was found that 1830's timber of the area was mostly oak species with smaller amounts of hickory, ash, maple and elm (Table 1). The average tree density was 1.5 per hectare on the uplands with an average basal area of 9.9 square decimeters per individual. Today the land is mostly forested except for upland farms. Compositional analysis of present forests (Blewett et al. 1983) indicates that oak species have dropped from 78 percent frequency among witness trees to less than 30 percent while elm and hickory species have become relatively more important. Most notable is the contemporary 10 percent frequency of redcedar in three sample stands totalling nearly 500 hectares, where no cedars were recorded as witness trees. Although the average tree size is now slightly less than it was 150 years ago, the tree density for the area is now approaching 300 per hectare (excluding upland farms).

DISCUSSION

The lack of witness tree records of redcedar in the Upper Mississippi region is probably an accurate reflection of redcedar's low population density in presettlement times. From the surveyors' notes of 1837 for Dubuque County (Table 1) it is clear that upland tree densities were very low and the dominant trees were fire resistant and dry tolerant oaks. Some farm clearing which began in the 1830's may have been a factor in the low tree density calculation, but most farm clearing did not begin until the 1840's. Trewartha (1940) indicated that Mississippi River valley and major stream valleys in eastern Iowa were heavily timbered, but uplands were prairie dominated. The open uplands strongly suggest a history of fire which would have restricted the redcedars primarily to fire-protected bluffs where they were described in historical accounts. Although it is possible that some surveyors may have ignored redcedars, cedar does appear as witness trees in some Missouri records (Personal communication from an anonymous conference participant). Furthermore, the author has found redcedars established on an old suface mining site that was abandoned about 1840 in Dubuque County where many cedars in a dense stand are in the range of 10 to 15 meters high and up to 0.6 meter in diameter. These trees have three times the average diameter of witness trees recorded in the same area. It seems unlikely that trees capable of such magnitude would have been ignored if they had been present in the survey area.

The patterns of redcedar distribution in an old lead mining area (Mines of Spain) studied by the author (Blewett et al. 1983) are consistent with the view that the redcedar population is largely a recent, fire-protected phenomenon. The redcedar is typically found on ridges and southerly exposures and is often surrounded by *Quercus macrocarpa* (bur oak). In many of these sites the canopy of redcedar is nearly closed and in some cases completely closed to form heavy shading of the understory. Under closed canopies prairie flora are mostly absent, but under partial canopies some hill prairie flora such as *Sorghastrum nutans* (Indian grass), *Andropogon scoparius* (little bluestem), *Bouteloua curtipendula* (side-oats grama grass), *Spiranthes magnicamporum* (Great Plains orchid), and an assortment of asters and goldenrods persist as an indication that the area was once kept open by fire.

Numerous redcedars have been found dead or barely alive in the midst of second growth forest on slopes that were logged to fuel steam boats, saw mills and lead smelters in the late 1800's. Such occurrences have even been found on north slopes where red oak is beginning to enter the canopy as the last of the redcedars die out.

Most remnant hill prairies in the Dubuque, Grant and Sauk county areas of Iowa and Wisconsin have been protected from fire and as a result redcedar is now uniformly common. Prairies which have been burned until recently have sparse populations of small redcedars. One large hill prairie in the City of Dubuque described by Hintz (1961) and well known by the author is quite atypical of contemporary hill prairies. It is devoid of redcedar except for one, half-meter tall individual that persists in limestone outcroppings. The site is an ideal redcedar habitat, but it continues to experience fire annually with a given point frequency of two or three years. This particular prairie is in excellent floristic condition not by foresighted management, but by the hands of pyromaniac adolescents.

It seems clear from observations over the last century as well as recent witness tree and community analyses that eastern redcedar has become quite abundant within its range. In the absence of fire remnant hill prairies in the Upper Mississippi region are threatened by the redcedar in two respects. First and most obvious is the shading effect as cedars become more abundant and approach closed canopy conditions. Although prairie flora have survived 20 to 30 years of shading in oak canopies in several Wisconsin Scientific Areas, the very dense crown potential of redcedar would allow little photosynthesis at ground level. Because redcedar seed is readily dispersed by birds, no area is free from this threat. The second potential threat exists from soils changes that are induced by redcedar. It has long been known (Arend 1950, Read and Walker 1950) that redcedar litter induces increases in pH, calcium content and soil porosity on acid soils. Such changes could have a profound influence on existing prairie flora. Blewett (1981) confirmed findings by Etherington (1975) that soil pH and soil moisture regime are the most reliable indicators of plant species distributions.

One final and positive attribute of the eastern redcedar's behavior is its potential use for the interpretation of landscape and landuse history. Because of its consistent habit of establishing itself on open habitat of almost any soil type, including abandoned surface mines, it can be used as an indicator of when the landscape was open or fields abandoned or when fire protection began. In hardwood forests on old logging sites it can be used to date the approximate time of clearing. In these cases one must assume an adequate seed source nearby, but our comparison of cedar populations in old fields, second growth forest, old mining sites and remnant hill prairies in and near the Mines of Spain (Blewett et al. 1983) resulted in a remarkable correspondence with known dates of land use history. Perhaps as a second positive attribute, we could again sustain the fence post and pencil industries as we try to save our remnant hill prairies in the prairie forest border region.

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INTRODUCED SEEDLINGS OF RED OAK IN A PRAIRIE HABITAT

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Abstract. An attempt was made to determine the survival rate of red oak seedlings introduced into a tall grass prairie habitat in a five-year study. About 300 acorns were planted directly in a warm-season tall grass prairie sod. During the first year a fair germination was observed but no noticeable stand of red oaks resulted. Thirty seedlings, one and two years old, from various seed sources were planted in two different locations. Seven of nine (77%) two-year-old seedlings from a Tennessee source, planted in an area providing more care, survived. Twenty-one other one- and two-year-old seedlings were planted in mostly smooth brome sod, but only four (19%) survived. Of 27 one-year-old seedlings from a germination test which were similarly planted in smooth brome sod, 12 (44%) survived. After five years of growth only two seedlings have exceeded one meter in height. Adverse factors included competition from grass, a grasshopper invasion in 1978, a May freeze in 1980, and grazing by rabbits and deer. No stand of red oaks was established in five years in either cool-season or warm-season tall grass prairie.

INTRODUCTION

According to distribution maps (Little 1971, Stephens 1973) the red oak, *Quercus rubra* L., is not native in Lancaster County, Nebraska, yet one may find an area near the southwestern suburb of Lincoln, Nebraska, where a few red oaks are included in a woodland. The red oaks have been estimated to be 150 to 200 years old, which would seem to indicate that they might in fact be native. In the edge of this wooded area young red oaks up to five cm in diameter are found growing in association with more sparse vegetation than that which occurs in native grassland areas.

The above authors indicated the presence of red oaks in Nebraska counties bordering the Missouri River south of South Sioux City, plus two interior adjacent counties. Earlier floras of Nebraska (Petersen 1923, Winter 1936) have indicated that the red oak is the second most common oak in the state, and its distribution is in the southeastern part of the state along the Missouri River and its tributaries.

The objective of this investigation was to ascertain whether red oaks could develop in brome grass or in warm-season tall grassland without relief from competition such as being planted in a prepared seed bed or transplant bed.

MATERIALS AND METHODS

In late May, 1977, about 350 red oak acorns were obtained. A sample of these was reserved for a germination test and the remainder, about 300 acorns, were planted in a warm-season tall grass prairie at the Reller Natural History Research Area (RNHRA) which had been planted in 1970 to five common prairie grasses: Indian grass (*Sorghastrum nutans* (L.) Nash), big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Andropogon scoparius* Michx.), switch grass (*Panicum virgatum* L.), and side oats grama (*Bouteloua curtipendula* (Michx.) Torr.). The area had been burned May 7, 1977, for the first time since its original planting and acorns were planted June 1, 1977. Acorns were dropped into wedge-shaped clefts in the soil which were then stamped closed with the heel of a shoe. The area was planted on a 3-meter grid plan. The area was 30 m wide and 81 m long. This produced eleven acorns in each of 27 rows which were 3 m apart.

About one year later, April 1978, thirty bare-rooted seedlings of red oak from various seed sources were planted at RNHRA. Nine, which were two-year-old seedlings from Tennessee, were planted around a crushed-rock parking area and thus had less shading from other vegetation, had occasional buckets of water put on them during hot dry periods, and were surrounded by chicken wire during winter. The other 21 seedlings, mostly one year old, were planted near a corner of the RNHRA adjacent to a road. Smooth brome had encroached and nearly dominated the area except for some young bur oak trees and a few clumps of native big bluestem.

In May 1978, 27 seedlings, which remained from seed germination tests run on more than 50 acorns from the previous year's planting, were added to the plot of 21 seedlings planted in the brome grass area. These seedlings, as with the others, were planted four meters apart in four rows that were six meters apart. Seedlings were planted directly into the sod without a prepared bed being made for them or without the use of herbicides to kill off the existing vegetation. These 27 were taken to the field in pots and the whole ball of soil planted.

In the first years of the investigation the four rows of seedlings were mowed twice a year. During later years at the times of observation, grass was pulled from the immediate area around the seedlings allowing measurements to be made. Data and measurements were taken in late May and early September for five years, but since all transplants which survived remained small and none became sapling size, the data were of little value.

OBSERVATIONS

In the areas where acorns were planted the growth of the tall grasses, particularly big bluestem and Indian grass, was phenomenal the first year of observation (1977). Since big bluestem is given a distinct stimulus the first season of growth after a burn it was not unusual that most inflorescences were produced on stems about two meters tall, with those at the lower end of the area in more moist soil being taller. Early in 1978 before the vegetative growth on the warm-season grasses had begun, a survey determined that a fair number of acorns had germinated, although their growth was distinctly limited by the abundant growth of the tall grasses. The young seedlings of red oak were effectively covered by grass again the second summer of growth. In the spring of 1979 and 1980 no evidence of a stand of red oaks was visible in the area. Before the April 1981 regular four-year cycle of burning, a search was made for seedlings of red oaks but none was found, yet a scattering of ash, elm, bur oak, and walnut were seen in the area.

The growth of the red oaks during the first two years was not rapid enough to keep them from being effectively smothered the next two years.

Of the thirty seedlings of various seed sources nine two-year-old seedlings from Tennessee that were planted around the laboratory of the RNHRA all had a successful first year of growth with substantial stems and several leaves. Grazing by rabbits was very severe during the first winter with some of the main stems being clipped off near ground level. Development was less vigorous during the second growing season. Two seedlings which had not shown much growth and a third which had been all but lost in an overgrowth of tall grasses were not protected by chicken wire during the second and third winters as the other six were. All three of these have subsequently died but one of the three still produced two leaves during the fifth year of observations. The six remaining seedlings which received some protection and added water varied in height from 30 to 100 cm. In the last two years of observations the branches above the chicken wire on two plants were eaten off by deer during the winter.

The remaining 21 of the 30 seedlings which were planted in smooth brome grass showed a diverse amount of growth, from some dying the first year to those few (only four) surviving until the end of the five years of observations. None became saplings and none showed vigorous growth during any year.

Twenty-seven seedlings from the seed germination test which were planted in the smooth brome area likewise showed great variations in growth. Some died the first year in the field and others showed moderate growth. Some died each year and at the end of the fifth year, in September 1982, only 12 of 27 seedlings were still surviving. One seedling had attained a height of 50 cm during the five years, but had only a few branches up to 30 cm at the end of the observations.

For a good part of the growing seasons the red oak seedlings were covered by the growth of smooth brome grass. Grasshoppers were a common pest during late summer and autumn most of the years of observation, but the invasion which occurred during the first year of growth was probably the worst. The second year of growth was better, but the May of 1980 freeze, after the leaves had expanded, caused great damage to most of the red oak plants. Of all the trees in the RNHRA only the elm trees showed little or no effect of the freeze. Many trees including ash and mulberry were entirely defoliated. No mature trees were observed to die from the freeze. Pockets of rabbit pellets around the base of several seedlings led to the suspicion that rabbits had clipped off some of the young seedlings close to the ground. In general two-year-old seedlings had a higher survival rate than the one-year-old seedlings.

SUMMARY AND CONCLUSIONS

The 300 red oak acorns which were planted among warm-season tall grasses produced no seedlings nor saplings at the end of four growing seasons.

One- and two-year-old seedlings of red oak introduced into cool-season smooth brome sod varied in survival rate depending on whether they were transplanted with bare roots (4 of 21 or 19%) or with roots in their potting soil (12 of 27 or 44%). Some bare-rooted two-year-old seedlings had been planted in an area covered by crushed rock. These had been watered, were not shaded by other vegetation, and were protected from grazing. Seven of nine (77%) of these survived. After five growing seasons 40% (25 of 57) of the introduced seedlings survived but none were thriving saplings.

ACKNOWLEDGEMENTS

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DISTRIBUTION PATTERNS OF PRAIRIE PLANT SPECIES IN A CLOSED-CANOPY FOREST SITUATION

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Abstract. Prairie plants are part of the woodland understory in lands adjacent to the former Grand Prairie in central Missouri. Though low in vigor, these plants grow from extensive, well-developed root systems. They are grouped in numerous scattered clusters beneath the woodland canopy, and their locations are highly predictable with respect to soil type and aspect. Distributions indicate that they are the result of dynamic interactions between forest and prairie, and that they maintain themselves by preserving root systems rather than by reproduction. Their distributions also provide insights concerning the fine structure of one type of forest/prairie transition.

INTRODUCTION

The tallgrass prairie occurs in a region that supports both forest and prairie. Where the two communities meet, vegetation elements usually intergrade (Bliss and Cox 1964, Bray 1960, Curtis and McIntosh 1951) rather than change abruptly (Dyksterhuis 1957). This creates a transition zone which has been variously described as broad (Anderson and Schwegman 1971, Ehrenreich and Crosby 1960, Vestal 1936), irregular (Weunscher and Valiunas 1967), and patchy on both large (Sears 1981) and small (Anderson 1983, Buell and Facey 1960, Forsyth 1981, Sears 1942) scales. Although little is recognizable today, once much of the region supported a vegetation which was not quite forest, and not quite prairie, but somewhere in between.

This was particularly true in Missouri, a prairie transition state (Schroeder 1981). Henry Rowe Schoolcraft (1955) wrote of the Ozark region in 1819: "a tall, thick, and rank growth of wild grass covers the whole country, in which the oaks are standing interspersed, like fruit trees in some well-cultivated orchard." More recently, Ray and Lawson (1955) described a forested Missouri Ozark region where "scattered prairie openings, natural clearings, glades, and rocky barrens occupy a considerable acreage," and Martin (1954) discussed the fairly heavy stands of native grasses beneath the "historically open, mature forest canopies."

Unfortunately, most of this landscape type has been lost because of clearing, grazing, and fire suppression. Although literature concerning it is equally scarce, several restoration projects are being undertaken (Iffrig and Nelson 1983, USFS personnel, personal communication). If indeed the transition between forest and prairie is recognized as a restorable landscape type, it is imperative that we better understand the ecological factors involved in the intermixing of these two communities.

This study, which grew from a more comprehensive prairie restoration project still underway, examines some of the local vegetation patterns in a forest/prairie transition zone. In particular, it relates survival of prairie plants in forest communities to successional processes in the Ozark border region.

BACKGROUND

In 1980, the National Forest Service cleared 50 acres of forest from a block of 160 acres of second-growth timber. It was located on the fringe of what once was known as the Grand Prairie, in Callaway County of north-central Missouri. The trees, which were 40 to 60 years old, were removed through the issuance of firewood cutting permits. No herbicide was applied, and approximately ten trees per acre were left standing. The goal of the Forest Service was to burn annually and hopefully produce a "savanna" appearance as the scattered prairie plants increased in number and vigor. Studies to date show that this is occurring (for example, see Fig. 1), but that the response differs according to soil type (Fig. 2). In fact, as is diagrammed in Fig. 3, prairie plants on this research site are distributed in association with certain topographical features. This study began as an attempt to locate prairie plants in the woodlands surrounding the original research site and identify patterns in their distribution.

PROCEDURE

To assist in identifying landscape features in the field, a small-scale shaded relief map of the study area was constructed from the local USGS topographic map. Several transects were marked on this map, each traversing the entire length of a forested ridge and approximating its contour. The transects were spaced about 20 meters apart, and thus the number per ridge varied. Each was traversed in the field and the locations of prairie plants marked, using the transect lines as reference points. Boundary lines were drawn around the clusters of prairie plants when the final copy was prepared. Similarly, areas dominated by species typical of old-field situations, and of shaded mesic forest situations, were located on the map.

After establishing the location of groups of prairie plants, we excavated several and examined their root systems. Included in this survey were six individual lead plants (*Amorpha canescens* Pursh.), two individual goat's rue (*Tephrosia virginiana* (L.) Pers.), three individual sensitive briars (*Schrankia uncinata* Willd.), and four yarrow colonies (*Achillea millefolium* L.). The root systems were removed, washed, measured, and photographed.

RESULTS

Prairie plants do exist in the woodlands of the study area, and in discernable patterns. Their locations, together with the locations of old-field and mesic forest species associations, are illustrated in Fig. 4. Understory communities in this latter category are found along the lower portions of the drainages and extend partway up the north- and east-facing slopes. Prairie associations occur on the narrow ridgetops and on high south- and west-facing slopes, just as they do on the nearby deforested area (Figs. 1 and 3). Old-field vegetation occupies positions intermediate between the two.

Preliminary results of the root studies are shown in Fig. 5. Lead plant *Amorpha canescens*) and goat's rue (*Tephrosia virginiana*) have long slender taproots which averaged 1.1 m and 0.5 m in length, respectively. Sensitive briar (*Schrankia uncinata*) has a large vertical taproot which averaged 2.5 cm in diameter at the crown and 0.6 m in length. Numerous secondary roots branched from the taproot. The yarrow (*Achillea millefolium*) colonies averaged 9.8 live root crowns and 6.5 dead root crowns per colony. Mean total rhizome length was 2.4 m.

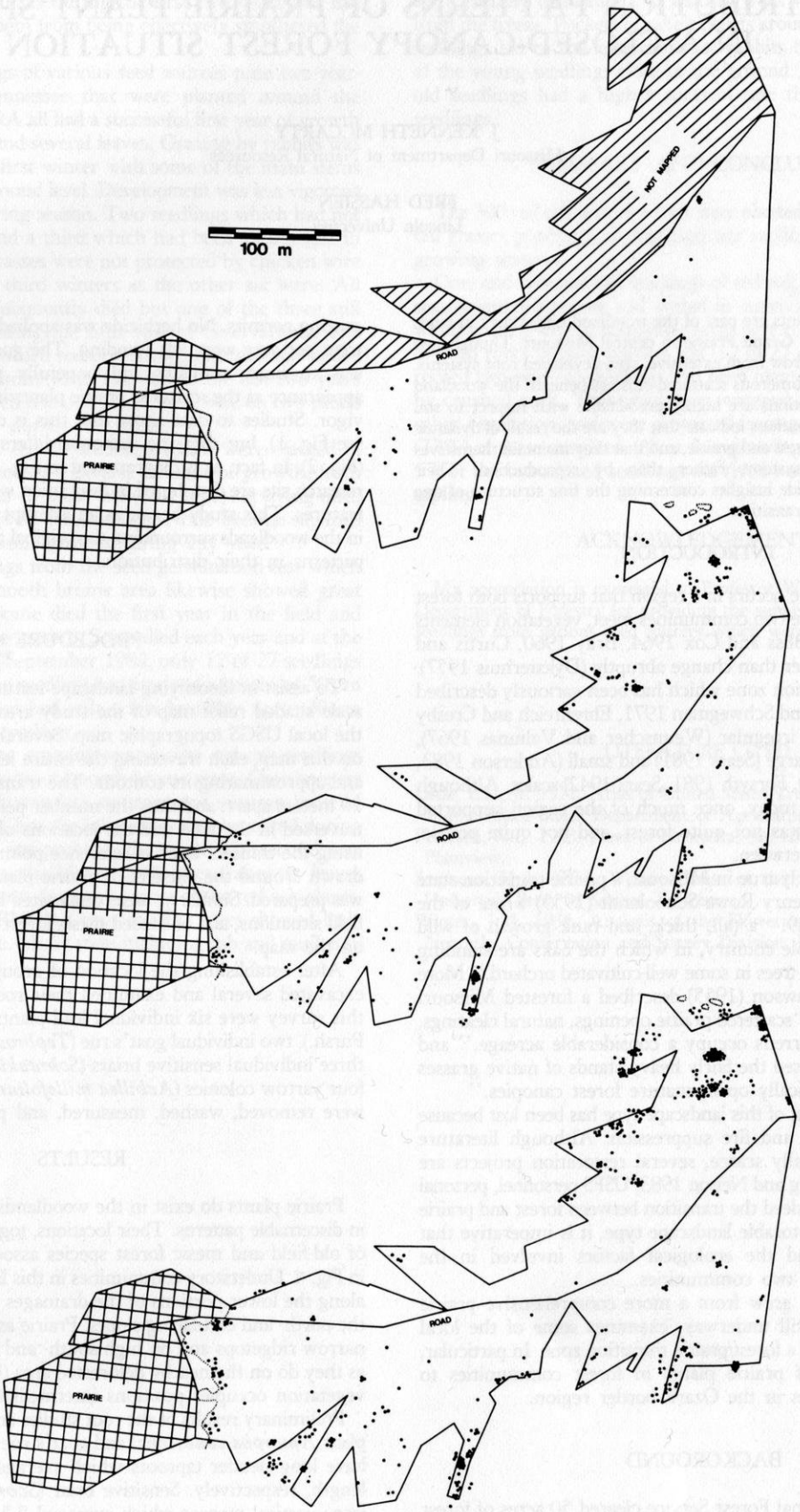

FIG. 1. Locations of clumps of big bluestem, little bluestem, and Indiangrass the first three years after tree removal on 50 acres of second growth timber in a prairie-forest transition zone.

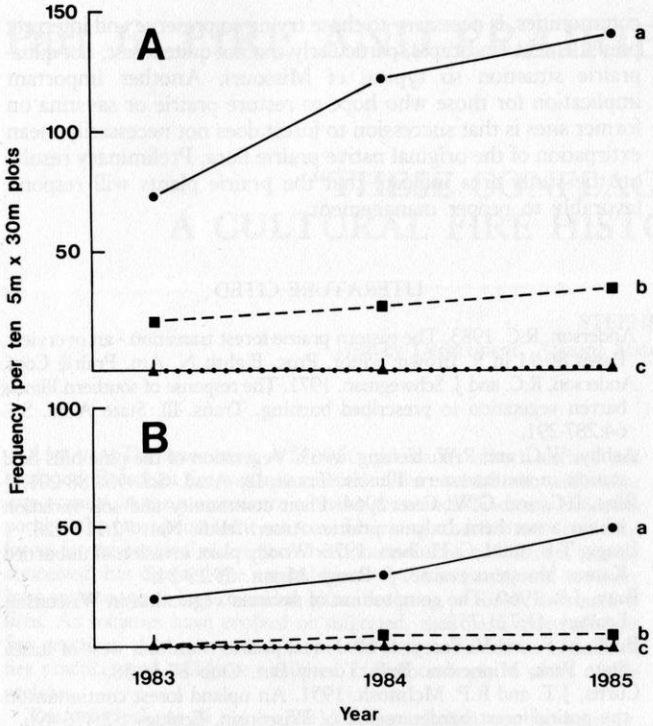

FIG. 2. A. Number of big bluestem clumps counted on the research plots of three soil types, 1983-1985.
B. Number of individual lead plants counted on the research plots of three soil types, 1983-1985.
Curve a: Hatton soil.
Curve b: Keswick soil.
Curve c: Gorin soil.

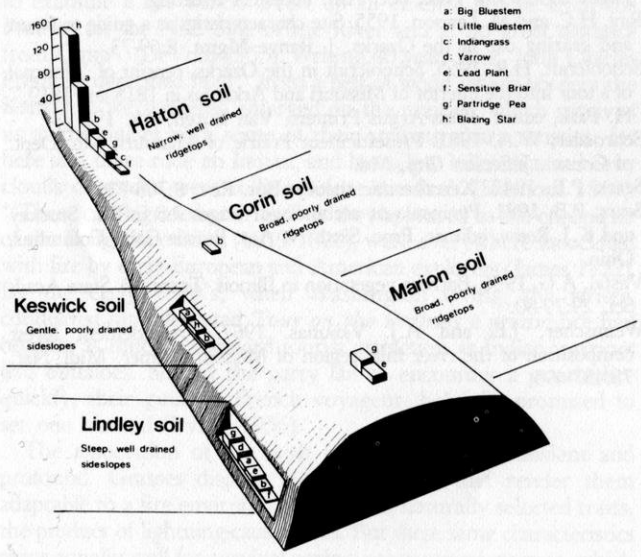

FIG. 3. Diagramatic representation of the relationships between soil type, drainage properties, topographic positioning, and frequency of selected prairie plants the first year after removing timber from 50 acres of second growth timber in a prairie-forest transition zone. Scale represents the number of plants per ten 5 meter x 30 meter research plots.

DISCUSSION

Our survey located numerous characteristic prairie plants growing in a woodland understory situation. Although they grew from extensive, robust, and presumably old root systems, most were inconspicuous because of limited flowering and production of only one or a very few leaves. They were never isolated but were always grouped with several others to form clusters, which were distributed in relation to local changes in soils, aspect, and topography (Figs. 1-4). Prairie plants were found only on narrow, well-drained ridgetops, and south- and west-facing slopes, high on the watershed. Similar relationships have been noted by several authors throughout the tallgrass prairie region (Ashby and Kelting 1963, Anderson 1983, Buell and Facey 1960, Forsyth 1981, Sears 1942).

The study site lies within a tension zone. This is indicated by soil types which are classified as forest but have certain prairie characteristics (SCS personnel, personal communication), the close proximity to documented presettlement prairie systems (Schroeder 1981), and close proximity to prairie soils. Succession is a dynamic process, and the islands of prairie plants found beneath the woodland canopies probably owe their existance to stronger prairie influence in the past. Forest closure displaces prairie species, but rates vary in dissected terrain (Bragg and Hulbert 1976). Though closure is complete on the study site, groups of prairie plants still occupy all of the well-drained or southerly-exposed locations. Vigor in all cases is much reduced from their open-grown counterparts, and site inspections and seedbank studies (Hassien and McCarty unpubl.) show that reproduction is scarce to non-existent. However, all plants examined grew from strong, well-developed root systems and probably have been present for some time. They are the extreme limit of prairie representation in the forest/prairie transition zone, and form a mosaic beyond the more noticeable islands of prairie recorded around the fringe of the prairie peninsula (Eyster-Smith 1983, Sears 1981).

Understanding the structure of forest/prairie transitions, and of the patterns of dynamic interactions between the two

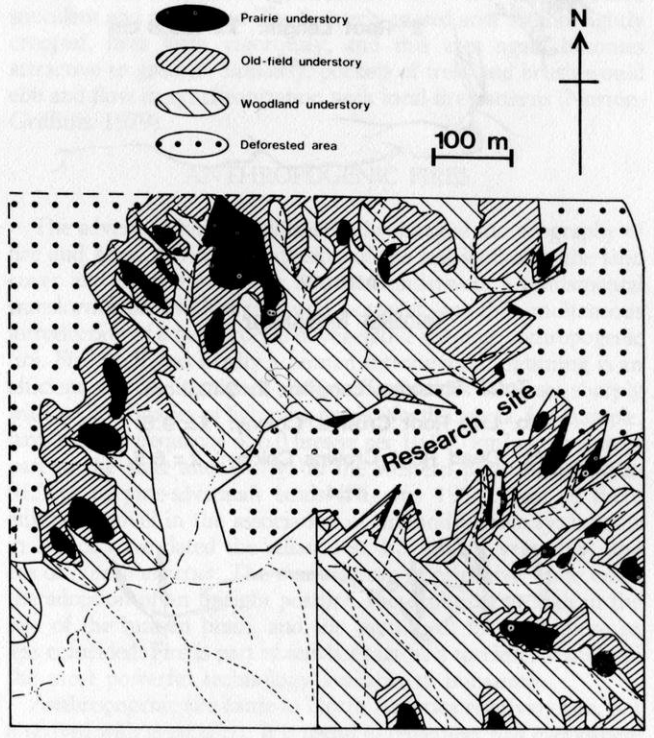

FIG. 4. Location of groups of prairie plants in the woodlands surrounding the original research site.

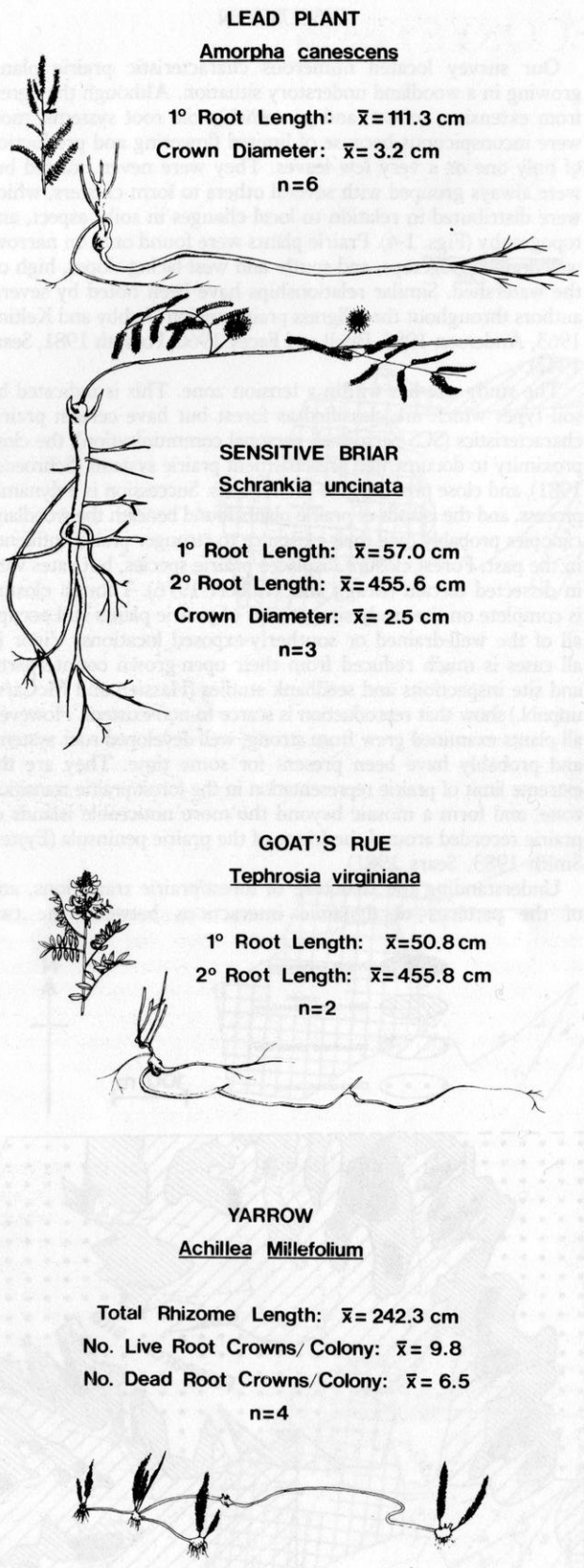

FIG. 5. Typical root structure and average dimensions for four species of prairie plants.

communities, is necessary to those trying to preserve and interpret presettlement landscapes, particularly the not-quite-forest, not-quite-prairie situation so typical of Missouri. Another important implication for those who hope to restore prairie or savanna on former sites is that succession to forest does not necessarily mean extirpation of the original native prairie flora. Preliminary results on the study area indicate that the prairie plants will respond favorably to proper management.

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Part 6. FIRE AND PRAIRIE ECOSYSTEMS

"THESE CONFLAGRATED PRAIRIES" A CULTURAL FIRE HISTORY OF THE GRASSLANDS

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Abstract. The association of fire with grasslands is both ancient and profound. Broadcast fire was instrumental in the establishment and, more importantly, in the maintenance of many grasslands. Since the Holocene perhaps the most prominent sources of burning, and the most powerful forces for the removal of fire, have been human. Cultural history, broadly conceived, has directed the natural history of American prairies; rarely have anthropogenic fires coincided, either in timing or effects, with natural fires. As societies have evolved or migrated, they have changed their fire practices. A single prairie may have been subjected to a series of fire practices and will have exhibited, correspondingly, a series of fire regimes.

The principal use of fire by the American Indian was for hunting. Grasslands were routinely burned, and tallgrass prairies were able to maintain themselves against reforestation pressures. The most important consequence of Euro-American settlement was the introduction of livestock (with overgrazing) and the conversion of prairie to farms, forests, and ranches, each of which evolved a suitable set of fire practices and all of which sought to regulate broadcast burning. In recent years interest in prescribed fires has revived for the management of nature preserves, for scientific research, and for limited aspects of range improvement.

FIG. 1. Charles Russell, "Crow Burning the Blackfoot Range" (1905).

INTRODUCTION

Shortly after reaching the Great Plains, the Lewis and Clark Expedition "sent Mr. Durione the Sioux interpreter & three men to examine a fire which threw up an emence Smoke from the Prairies on the N.E. Side of the River and at no great distance from Camp" (DeVoto 1953). Writing 40 years later, John Charles Fremont described how "from a belt of wood which borders the Kansas ... we suddenly emerged on the prairies, which received us at the outset with some of their striking characteristics; for here and there rode an Indian, and but a few miles distant heavy clouds of smoke were rolling before the fire" (Fremont 1845). "These conflagrated prairies," as they appeared to the chronicler of the Long Expedition (1819-1820), were everywhere associated with fire by early European and American explorers (James 1822). By the early 1830's, when Washington Irving, the writer, conducted his celebrated *Tour on the Prairies* a prairie fire had become as much a standard tourist attraction as Indian warriors and buffaloes. Should the party fail to encounter a prairie fire quickly, their guide, a French voyageur, helpfully promised to set one himself (Irving 1956).

The association of fire with grasslands is both ancient and profound. Grasses display many attributes that render them adaptable to a fire environment - in part, naturally selected traits, the product of lightning-caused fires. But these same characteristics serve equally well for survival against other prairie stresses, which often coincide with fire. They are part of a suite of selected traits that adapt the plants against drought, cropping, and fire. They seem to have no single selection source, and no uniquely selected properties. Fire is one of a complex of environmental considerations, and fire-adapted traits, part of an ensemble of useful characteristics. Studies of grazing and fire in the Serengeti show perhaps how an integrated cycle of grazing and fire can function. Heavy grazing by large herds of ungulates reduces the grass cover locally so that it burns poorly, if at all. The next season the herds move on to areas that were successfully burned, where the grass is more succulent and nutritious. The formerly grazed area is more lightly cropped, fires burn vigorously, and this area again becomes attractive to grazers. Similarly, pockets of trees and brush would ebb and flow in synchronization with local fire patterns (Norton-Griffiths 1979).

ANTHROPOGENIC FIRES

The advent of humans dramatically changed the geography of fire and grass. With the recession of the last icesheets, the land cover and climate of North America underwent a fundamental transformation. No less profound, however, was the simultaneous introduction of a new process of vegetative shaping: anthropogenic fire. Fire itself was hardly a human introduction; lightning is an efficient source of ignition, and its effectiveness increases sharply with aridity. Studies of lightning fire in North Dakota, for example, have found a frequency of 6.0 fires/yr per 10,000 km^2 in the eastern part of the state and 24.7/yr in the western part, escalating to 91.7/yr in pine-savannah lands (Higgins 1984). Nor is there anything novel in the association of fire and humanity; hearths in Africa have dated the alliance at 1.8 million years b.p., the era of *Homo erectus*. The manufacture of primitive stone tools, the adoption of an upright posture, the explosive growth in the size of the human brain, and the capture of fire - all more or less coincided. Fire is part of our heritage as a species, for millenia the most powerful technology available to humanity.

Anthropogenic fire came to North America relatively late, but it arrived with great effect. It is useful to remember that everywhere grass is the primary fine fuel available for broadcast fire. Because grasses carried fire and were adapted to fire, they were generally favored by the introduction of the more wide-ranging and more

FIG. 2. Alfred Jacob Miller, "Prairie on Fire" (1836). Note the foreground activity, in which backfires are being set around the camp and then swatted out on the inner side.

frequent burning that accompanied human migration. It is no less important to distinguish between fire as a creator of grasslands and fire as a perpetuator of grasslands. It is both - has been both. It is not necessary to make fire the sole originator of the North American grasslands. A combination of fire, climatic warming, and vegetative adjustments following the recession of the icesheets no doubt brought about the contiguous grasslands of the Great Plains. Almost certainly, however, anthropogenic fire was responsible for maintaining those grasslands. Without fire most of the grasslands - especially those east of the High Plains - would have been submerged beneath a subsequent invasion of woody plants (Clouser 1978). This was not, strictly speaking, a natural cycle of fire: the extent, the timing, and the purposes of anthropogenic fires differed somewhat from those of a lightning fire regime. Anthropogenic fires clustered in the spring and, especially, the fall, somewhat outside the pattern of summer thunderstorms (Moore 1972).

AMERICAN INDIAN FIRE PRACTICES

At first blush it seems fantastic that early man in the New World - small bands of nomadic, big game hunters - could have had the power to influence the landscape on anything like this scale, that early man could have sustained grasslands in partial defiance of climatic changes. Yet broadcast fire was an adequate tool; and there was much to gain and remarkably little to lose from firing the landscape. The reasons for broadcast fire which humans had discovered over the course of nearly two million years were still valid. It is impossible to imagine a human society without fire, and the more technologically primitive a society, the more powerful is fire as an all-purpose tool for domestic use, warfare, ritual, hunting and gathering, farming and herding (Pyne 1982). Almost universally, too, fire was left to burn under conditions that, by contemporary standards, amount to carelessness. In puzzling through the apparent extensiveness of anthropogenic fire and its consequences, remember that fire propagates, that fire effects multiply and spread, and that, once established, a grassland can be maintained almost indefinitely through the intelligent application of fire. Nor was the absence of an easy mode of transportation an impediment to burning on a colossal scale. In historic times aborigines in Australia routinely burned all but the dampest rainforest, and the peoples of sub-Sahara Africa fired grasslands, savannahs, and portions of forest annually (Nicholson 1981, Hall 1984, Lewis 1985).

Of all Indian uses for fire, the most widespread was fire for hunting. Recognizing that new grass sprouting on a freshly burned site would attract grazers by its superior palatability, Indians could control large-scale movement of herds by alternately firing and greening up sites and, on a smaller scale, could hunt individual animals by placing snare traps over burned plots - in effect, baiting the trap with fired grass. The Apaches worked a variant, using smoke to lure deer driven mad by flies. Fire hunting, properly speaking - that is, the strategy of surrounding or driving the principal grazers of a region by fire - was universal. In the East it was used for deer; in the Everglades, for alligators; on the prairies, for buffalo; along the floodplains of the Colorado River, for rabbits and wood rats; in Utah and the intermountain region, for deer and antelope; in the Great Basin, for grasshoppers, in California and the Southwest, for rabbits; in Alaska, for muskrats and moose. It is, in fact, a remarkable coincidence that virtually all the fauna prized as game come from environments that are sustained by periodic fire. Special hunting sites, often extensive, were maintained and visited in the course of an annual cycle which typically included burning in the autumn. Many of these sites had at one time been

wooded and were capable of supporting forest; the land had been cleared either by centuries of swidden cultivation followed by fire or by a combination of broadcast fire and a warmer, drier climate; either way, once converted to grass, broadcast fire in association with hunting could maintain the site as a grassland. In this way, too, the practice of a late fall hunt - a cultural necessity to provide food for the winter - altered the natural pattern of ignition, which had depended on spring and summer thunderstorms. Both the range and timing of a natural fire regime were affected.

Fire hunting thus not only served as a tactic of harvesting but as a means of sustaining (and even creating) the habitat upon which it depended. Tribes burned nearly all areas that could support fire, leaving many savannahs or "barrens" or, where forests persisted, relatively open woods free of underbrush. The dense, impenetrable forests of precolumbian America thrived in bogs, swamps, poorly drained lowlands, where standing water protected trees from annual fires. The grassy openings - often referred to as "deserts" by Europeans, implying a wooded place that had been cleared or maintained by humans and then deserted - were ubiquitous. As one moved inland from the humid east into slightly more arid lands, less densely inscribed by streams and littered by bogs, the continuity of grasslands improved. Small clearings became large clearings; large clearings merged, with strips of forest restricted to river banks; extensive prairie peninsulas opened up into the central plains. Here climate, topography, and anthropogenic fire combined to make the Great American Desert.

Actually this progression should be reversed. The fires almost certainly appeared first among the shortgrass vegetation of the High Plains, then, powered by the westerlies and the normal tracks of spring and fall storms, radiated eastward. As more humid, more topographically varied, more poorly drained sites were encountered, large fires could not be sustained. Even in the 20th century it was possible to have fires of 6 million acres or so on the High Plains; fires of similar extent were almost certainly typical of presettlement times. But no such fire could occur further to the east. The continuity of the fire environment broke down, individual sites of much smaller dimensions would have to be separately fired, and grasslands became intermingled with bogs and woods in a complex mosaic of climate, vegetation, and human manipulation. Still there were areas - prairie peninsulas - remarkably extensive, which athropogenic fire sustained. And further east there were more or less isolated barrens, famous as hunting grounds, until, with fire exclusion, they passed into woods. Within the contiguous grasslands there remained relic enclaves of trees, protected by meandering streams and rocky bluffs; in almost all cases, these sites were shielded from fires emanating in the west. A smaller number of large fires, some ignited by lightning, could keep the western grasslands intact; further east, the cycle of firing would become almost annual, and the proportion of anthropogenic fire would be nearly total.

FIG. 3. Fighting a prairie fire, Ouachita National Forest, Oklahoma (1910). In addition to wet blankets, sprinklers, and (occasionally) buckets, plows and drags were commonly used. Courtesy US Forest Service.

Fire practices require fire control as well as fire use. Without the ability to stop fires, the power to start them yields only a kind of opportunism or vandalism. The American Indian did practice fire control, adequate to the needs of his society. Wildfires that threatened an encampment would be met by backfires, blankets, even (for some tribes) special long-handled clubs for beating flames. Buffalo hides sometimes served as protective shelters for Indians trapped by fast-moving prairie fires. Precautions were taken not to camp in tall grass or to allow a cooking fire to escape while a party was present, though the fire itself was rarely extinguished. There were failures, like the Yankton camp overrun by an evening fire in 1868 that swept through sixty tipis and took nine lives (Lekness 1983). But the chief weapon the Plains Indian possessed for fire control was his nomadism. He could simply move on, following the herds. His use of fire was often at sites some distance from his home grounds. Without a fixed land base, the standards for fire contol were flexible and the opportunities for fire use extensive.

Such fire practices were not unique to the American Indian, nor were their effects. The Seminole practice of hunting alligators with fire is identical to the Indonesian method of hunting crocodiles; the Iroquois practiced swidden agriculture in much the same way as do modern peasants in northern Thailand and did Scandinavians up to the 20th century. Pasturage fires for wildlife in America are indistinguishable from those set on the steppes of central Asia, on the veldt of East Africa, or on kangaroo ranges in Australia. Ancient Scythians on the Asian steppes and aborigines along the Austalian coast used broadcast fire as a weapon in much the same way that the Sioux and Comanche used it on the Great Plains. Of course, even within North America, there were variations in fire practices among tribes and variations within the history of a single tribe. Yet this general panorama of Indian fire practices is almost certainly correct, and it was from the American Indian that the American European acquired many of his own fire practices.

Whether the grasslands of North America, as a whole, were expanding or contracting at the time of European discovery is difficult to say. There is evidence - eyewitness reports - of deforestation by fire, of "deadings" created during times of drought which were then perpetuated as prairie by broadcast fire. Most of those who puzzled over the origins of the grasslands had little doubt that they originated from Indian fire practices. Thomas Jefferson suggested that "fire hunting" - practices by all the tribes known to him - was the "most probable cause of the origin and extension of the vast prairies in the western country" (Jefferson 1952). Writing in 1819 Robert Wells surmised that "ordinarily, all the country, of a nature to become prairie, is already in that state; yet the writer ... has seen, in the country between the Mississippi and Missouri, after unusual dry seasons, more than

one hundred acres of woodland together converted into prairie. And again, where the grass has been depastured by large herds of domestic cattle, it will assume, in a few years, the appearance of a young forest'' (Wells 1819). Francois Andre Michaux reported similar processes at work in the famous Barrens region. ''Every year, in the course of the months of March or April, the inhabitants set fire to the grass.'' The ''custom of burning the meadows was formerly practiced by the natives, who came in part to this part of the country to hunt ...'' To this cause Michaux attributed the ''birth'' and ''maintenance'' of the ''spacious meadows in Kentucky and Tennessee'' (Michaux 1805).

But quite apart from the question of grasslands expansion, fire was responsible for sustaining the existing and relic grasslands. Of this there can be little doubt. Nearly everywhere - from Massachusetts to the Carolinas, to Illinois and Tennessee, to Oregon and Arizona - Euro-Americans reported trees springing up with settlement; the suppression of Indian and frontier fire habits encouraged a spontaneous process of reforestation, a reclamation by woody species of all sorts. The pace of reclamation varied with climate - far more rapid in the humid east than in the arid west - and with the intensity of other anthropogenic activities, such as herding and farming (Pyne 1982). Some of the refugia that had previously harbored trees were destroyed by draining and felling during settlement, but many enclaves survived and they provided source trees and brush for the reoccupation of the grasslands. A particularly instructive example is the early 19th century situation at St. Louis. When it was first settled, the village occupied a broad prairie. In time, as Indians retreated further west, as roads and plowed fields broke up the continuity of grassy fuels, and as heavy grazing by cattle eliminated the primary fine fuel, fires disappeared and trees sprang up; the closer to the town, the greater the density of reforestation (Wells 1819).

EURO-AMERICAN FIRE PRACTICES

The fire practices adopted from the Plains Indian were means for surviving in a permanent grassland fire regime. They were techniques for transients - for trappers, hunters, explorers, military expeditions, sportsmen, and teamsters. But the character of Euro-American settlement meant that such practices would serve only a transitional phase in the occupation of the Great Plains. The long-range settlement of the grasslands replaced nomads with settlers and converted wildland to farms, fields, and forest plantations. Domestic cereals replaced wild grasses; domesticated livestock, wildlife; woody species, the tall and short grass prairies; and agricultural fire, wild fire. The fire history of the grasslands becomes, by and large, a history of fuels conversion. New fire practices would have to be adapted or invented.

It is instructive that the first fire codes in the colonies prescribed certain seasons for burning and regulated fire hunting, which settlers had learned from Indians and applied with devastating effect (Dana 1956). Both injunctions were means of protecting established farms and towns from broadcast burning at the hands of hunters and semi-nomadic herders. To secure farms and fields, sedentary settlers found it necessary to practice protective burning - setting backfires in response to broadcast hunting and escape fires. In this way, a fire set for any reason at one site rapidly multiplied across the landscape, and the most promiscuous fire user determined the timing and extensiveness of fire everywhere in the region. The only long-term solution was to replace that whole set of fire practices - and the socio-economic system that sustained it - with another set.

AGRICULTURAL FIRE PRACTICES

Of all the new land uses, farming introduced perhaps the most complete transformation. Whether the farms raised commodity crops or livestock, they quickly intensified, following the example of Western Europe. Even livestock was farmed rather than ranched.

FIG. 4. Fire wagon and crew, Ouachita National Forest, Oklahoma (1910). Courtesy US Forest Service.

Special pasture grasses were planted, especially for dairy cows; cattle and hogs (in the 20th century) were fed on hybrid tallgrasses, like corn; the demands of clean-furrow feed crops and the restrictions on free-roaming stock left little room for free-burning fire. This was in contrast to the South and portions of the West where open range and transhumance followed Mediterranean herding practices and habits of fire use. The full agricultural reclamation of the grasslands had to wait for the industrial revolution - for its barbed wire, windmills, and fossil fuels; for its railroads, which tied interior farms to markets; for its fertilizers, which made possible the abandonment of forest farms, with their source of nutrient-rich ash. But the relocation of American farms from forested environments to grasslands would become one of the fundamental events of American agriculture. In mid-19th century America, most farms were on former woodlands; today, they occupy former grasslands. Through means that were both accidental and deliberate, agricultural reclamation would also profoundly rework the existing fire regime.

With the extension of settlement the expansive continuity of the grasses disintegrated. Roads, fields, plowed firebreaks, heavy cropping by cattle - all broke up the unity of fuels, the ease which broadcast fire could spread, and the biotic pressure that kept trees and brush from overrunning grasses. Gradually, domestic grasses replaced wild grasses, and controlled burning of stubble replaced prairie fires as a means of improving pasturage and controlling weeds. In other areas European pasture grasses and haying substituted for native grasses and fire. A new cycle of burning was initiated, one integrated into the rhythm of agriculture rather than that of nomadic hunting and gathering. Many of these practices had long-standing European precedents. Yet as American farming further intensified, even this arena shriveled. Open burning was too imprecise to assist close cultivation, the crowding of land ownership made escape fires too costly, and fuel loads (after intense utilization) were too light to carry flame.

And of course there were direct attempts to systematize fire practices and to control fire. The initial reaction to prairie fires - especially by recent immigrants from Europe - seems to have been paralysis. Perhaps the scale as well as the novelty was simply too great. Eventually, settlers organized fire brigades, fire codes attempted to regulate the burning of private and common land, and highly flammable fuels were replaced by less volatile vegetation. Confronted with wildfire, farmers plowed firebreaks around their fields at critical times; fought fires with plowed firelines, backfires, blankets, and sprinklers; tried to regulate the firing of pasturage and the irresponsible conduct of transients. The ultimate form of fire control was the conversion of wildland to rural land, followed by industrialization, which substituted mechanical and chemical treatments for open burning. Combustion remained fundamental

to the energy flow of the ecosystem, but it resided in the cylinders of tractor engines rather than the free-burning flames of open fires. Grass fires - which even in the 1880's had swept over vast acreages of the Great Plains and obliterated whole towns - became a rare event, no longer a wildland fire but a rural fire restricted to scattered fields, barns, and relic pockets of prairie and woods range. What had been an environment of frequent, often wide-ranging fires became one of intermittent, rigidly circumscribed burning. No other fire regime in the U.S. has experienced a more thorough transformation.

The critical period was the transitional phase. Here often incompatible fire practices, new ignition sources and mixed rules, old environments and new immigrants, all intermingled. Farmers and hunters, and farmers and ranchers, viewed fire differently. A controlled fire for nomadic hunters could be a wildfire for sedentary farmers; a society based on fixed land titles and crops carefully cultivated at a single site could not tolerate broadcast burning. Where land - common land, wooded land - was to be kept as pasturage, then fire could be used. Fire might also be employed, temporarily, to battle the wild elements retained within a half-settled landscape; prairie lands around a farm might be burned off to protect fields from wildfire, and pyres (or sometimes broadcast fire) might be lit to drive off plagues of grasshppers. Settlement, too, introduced fire sources and fuels previously unknown to the grasslands. Exotic vegetation like cheat grass and Russian thistle increased the flammability of many sites; dry cow chips, sailing like flaming frisbees before the wind added new modes of fire propagation (Haley 1929); and the railroad, upon which the settlement of the interior was so dependent, ignited prodigious numbers of fires until the surrounding wildland was brought into cultivation and the threat of legal action controlled the effluence of sparks that showered from smokestacks and brakes. In time, a prairie fire became a freakish visitation from wild nature, like a tornado, an unwelcome emissary from a more mobile social order or a transient reminder that settlement was not yet completed. Not surprisingly most of the devastating prairie fires of the historic record occurred during the transition from prairie to farm.

FORESTRY FIRE PRACTICES

In other areas, forests replaced grasslands. Much of this conversion occurred inadvertently. By eliminating the sources and fuels upon which broadcast fire depended, settlement merely liberated the natural pressures for reforestation. So univerally has this been the case that trees, both native and imported, might be considered as one of those symbiotic exotics, like honey bees and smallpox, that accompanied Euro-American settlement. Probably the most powerful mechanism in this transformation has been the introduction of exotic fauna in the form of domesticated livestock. All of the domesticated grazers and browsers now present in North America were introduced by the Europeans. Overgrazing became possible where it had not been feasible under the regime of the American Indian. The Indian had been able to expand somewhat the range of native species, but he could not effectively increase their density; he could not overgraze in a systematic way. The Euro-American could, and did. No other single process contributed so much to a change in the fuel properties, and thereby the fire properties, of the grassland. The elimination of copious abundances of grass everywhere made broadcast fire difficult. On a national scale the grasslands, relative to woodlands, went into a recession from which they have never fully recovered. In general, the outcome of the Indian settlement of North America was an expansion of grassland at the expense of forests; the outcome of European settlement has been an enlargement of forests (or woody vegetation) at the expense of grasslands.

In other areas, trees were planted - orchards in the more humid east, and conifer forests in the semi-arid west. It was hoped that afforestation would bring a welcome supply of wood to otherwise deficient areas, that forest influences would encourage a general amelioration of climate. The sand hills were especially attractive sites, and Nebraska - the unlikely originator of Arbor Day - was perhaps the most active propagandizer. The common observation that woody plants spontaneously generated in the grasslands encouraged those who, for one reason or another, wanted forests on the plains. From the onset it was recognized that prairie fires were the principal threat to forestation projects, that fire (not climate in the abstract) was the most likely cause for the deforestation that historically existed. In 1905 and again in 1910 grass fires obliterated the young plantations on the Nebraska National Forest. Eventually an elaborate system of fuelbreaks was established; that network, along with heavy, controlled grazing, reduced the fire threat to manageable proportions (Davis 1951). Later attempts at afforestation, notably the shelterbelt program, occurred in a different context, when prairie fires were largely a historic memory.

RANCHING FIRE PRACTICES

Not all of the grasslands were submerged into commodity farms or converted into new forests, of course. Many became ranches, and others, wildlands for recreation, wildlife habitat, or parks. In all of these instances, the grasslands would retain their generic identity as grasslands. With few exceptions - the Flint Hills region of Kansas perhaps the best known - ranchers on the Plains considered wildfires a scourge. Spring fires might be tolerated; fall fires never. Fires caused a temporary loss of pasturage, an acute problem when stock was held on the range over winter or when there was insufficient unburned range left to feed stock until greenup could follow. Fires required roundups and the transfer of cattle to unburned regions, and they compelled ranch hands to abandon other jobs and control the burn. The Indian practice of burning for habitat and hunting had been predicated on nomadism; such an existence could be approximated for a while by ranchers or drovers operating on public land under open range laws. But as the range closed, so did the opportunity for fire.

The antecedents for the cattle industry on the Plains had derived from the American South and portions of Europe, like Scotland and Spain, where broadcast fire was used annually, even promiscuously. In early 20th-century Florida, for example, still

FIG. 5. Burning out a firebreak. Nebraska National Forest, circa 1930s. The techniques were developed during the 19th century, but the equipment and purposes have been modernized. A tractor now pulls the plow, and instead of protecting winter forage, the firebreaks are intended to safeguard pine plantations on the Sand Hills. With adequate fire control, a pine forest was established. Today, heavy grazing of understory grasses is employed to reduce fuels. Courtesy US Forest Service.

a bastion of open range ranching, it is said that 105% of the state burned in a single year - the improbable figure resulting from the double burning, spring and fall, of the same areas. Similarly, on the public lands of the West, subject to transhumance and open range laws, firing was commonplace; herders fought bitterly with foresters to retain the use of broadcast burning. Ranchers on the Plains, however, became firm, almost hysterical advocates of fire exclusion. Those areas that perpetuated a tradition of fire use did so because they practiced different ranching strategies, for example, using the range only as a summer feedlot for calves that would be sold at the end of the season rather than kept over the winter. But the consensus of herding practices demanded a reform in fire practices, and ranchers actively fought fires.

This was serious business. "Orders were to go to any fire within a radius of a hundred miles," recalled one cowboy with the XIT ranch in Texas. Failure to respond was "sufficient cause for dismissal" (Duke and Frantz 1961). After the XIT was devastated by massive fires in 1885 - with an almost 25% loss among its herds - management instituted a system of plowed fuelbreaks or "fire guards." In September teams of three men were sent out; two or three strips were plowed about 100 feet apart; then from mid-November to mid-December the intervening grasses between the furrows were burned by horsemen dragging fire with oil-soaked ropes while others swatted flames that might leap across the furrows. Within a year 1,000 miles of fire guards were emplaced. During periods of extreme danger a cowboy would frequently man a high windmill tower to spot for smokes. Strict rules against careless fires, including smoking regulations, went into effect at critical times. Arson was punished severely, and stiff civil penalties could be brought against those ranchers whose negligence allowed fires to escape onto neighbors' lands.

"I guess [firefighting] and haying was the hardest work we did," recalled one cowboy, "or it was what we hated worse anyway" (Haley 1929). If the fire was small, it would be attacked directly with blankets, sacks, brooms, and chaps. If it was large or rapidly moving, it was worked along the flanks or halted by backfires from some fixed line. When enough men arrived, they would use a beef drag. The nearest steer would be slaughtered, split open, and pulled across the flames by a horse on each side. Behind the drag men were placed in relays every hundred yards to fight out the little spots of fire left behind. Where fires were a common problem, special chain drags were developed; large hides and water barrels were kept handy on fire wagons; and chuck wagons were prepared to keep crews in the field for several days. Many of the techniques developed to control range fires were subsequently transferred to forest reserves by dispossessed cowboys. Terms like "corralling" or "loose herding" forest fires testify to the heritage from ranchers to wildland fire control - a legacy that contrasts ironically with that far more ancient patrimony of broadcast fire left by herders in both the New World and the Old. The remark of the Plains cowboy who said of a burned range that "it shore looks like hell with the folks moved out" would have been unintelligible to the millenia of herders who preceded him (Adams 1948).

Accordingly, all grass fires were considered wildfires. There are numerous records of incendiary fires, for example - including many set by the Sioux to interrupt large trail drives in the Dakotas - but little use of fire for range improvement. Even in Texas, where the fire practices of the South and Spain merged, stringent legislation was passed in the 1870's to attack arson fire and eliminate escape fires. Instead, with closure of the open range, the incentives for burning also vanished. Liability for escaped fires, the absence of alternate pastures, the substitution of European pasture grasses for native species, the accidental introduction of exotic pyrophytes like cheat grass, the economics of feedlot fattening, and intensive utilization of grass - all discouraged controlled burning (Vogl 1974). Although a small revival of fire use has occurred over the past decade, ranchers use fire principally to eradicate noxious weeds, to convert brush to pasturage, and to retard encroachment by woody species - in brief, to enlarge the potential range. Once established, pasture lands, like farmlands, tend to experience a gradual reduction in the use of open burning in favor of mechanical or chemical treatments.

WILDLAND FIRE SCIENCE

Nor did the sciences support the practice of prescribed fire. On the contrary, the emergence of professional forestry early in the 20th century countered frontier folk knowledge, which held that grass fires could be useful, with seemingly scientific knowledge that all fires were destructive. Foresters became rabid critics of burning, not only in the woods but in virtually all biotas. Thus even in the realm of ideas trees triumphed over grass. Until the 1960's the Forest Service exercised a virtual monopoly on wildland fire research. There were exceptions, of course - places where traditional burning persisted or was reintroduced to restore native biotas, and people who persevered in the study (and advocacy) of broadcast fire. For the most part, they were isolated academic botanists (like John Curtis), folk practitioners, and assorted wildlife biologists (like Herbert Stoddard). The skills were never completely lost. It is a curious truth, in fact, that over the years the arguments for fire and the observations that supported them did not really alter much. What changed was the broader cultural context of those data and arguments. No longer folklore but science explained fire ecology, no longer utilitarian needs but historical preservation gave reasons for burning, and not folk practitioners but professional land managers held the torch. However, it was not until forestry, under the compulsions of the Wilderness Act, converted to the value of natural fire in wilderness areas, and then to prescribed fire at large, that the final objections to prairie fires were removed (Pyne 1985). Since then the scientific literature on fire ecology has grown exponentially, and grassland scientists have joined wilderness enthusiasts as advocates of prairie burning.

CONTEMPORARY FIRE PRACTICES

The most likely arenas for broadcast fire in the future are those areas, and those purposes, that mimic the past. Where prairies are to be restored to something approximating their original composition and structure, where grasslands are to be perpetuated as habitat for wildlife, where they are retained as grasslands for recreational values, parks, wilderness - there broadcast fire is not only useful, but mandatory. It has proved almost impossible to reestablish tallgrass prairies that resemble precolumbian grasslands without fire; and fire has demonstrated that it can be a manageable, cheap, and effective agent for promoting native grasses over exotics and for checking the invasion of grasslands by brush and trees. With respect to the management of fire in grasslands, the informing question is no longer fire control but fire use.

This is not simply a case of environmental restoration. Some of the techniques used resemble those employed in past eons, and some of the purposes recall those of other, older societies. Yet the outcome will be a new, unprecedented set of fire practices, purposes, and prairies. Fires burn in a cultural environment no less than a natural environment. Since the Pleistocene migrations of humans to North America, grasslands have become very largely a cultural artifact, and a fire burning today - even one intended to imitate historic processes and burning native grasses - is a new kind of fire, distinct from those of the past. If a fire history of the grasslands says anything, it is that fire is intrinsic to native prairies of the New World, that the principal source of that fire has been anthropogenic, and that the fire regime, including the structure and composition of its grassy fuels, has varied with cultural history. Modern fires occupy a different legal and institutional environment, with questions of liability and ownership; burns within a different intellectual environment, thick with new scientific concepts and environmental perceptions; shapes a different landscape, culturally distinct and often ecologically unprecedented.

Modern fire management must operate under constraints more formidable than any standards of the past. The nomadism that made broadcast fire so attractive to precolumbian peoples - a nomadism which was, in fact, demanded by their use of broadcast fire - is not available to modern managers. At all levels, especially where government agencies are involved, management demands a state of sophistication unimaginable to those who distributed fire before. (Interestingly, the most active advocates of prairie fires, the scientist and the tourist, constitute new categories of nomads.)

There seems to be no inherent pattern in grassland burning: it is enough that the grass be burned. Grasslands have been successfully fired in different seasons and with different intensities, with each resulting type a dutiful reflection of the society that controlled that particular fire regime - its fuels and ignitons. Contemporary ideas about naturalness, expectations about what the grasslands ought to be, and nearly two decades of intensive debate and research on the relationship between fire and wilderness assure us that prescribed fire will undoubtedly be fundamental to the management of that special category of grassland, the prairie. The outcome, a seemingly native grassland, will be in reality an artifact, a peculiar hybrid of nature and culture fashioned by another hybrid of nature and culture, fire.

The rewards, too, will be as much cultural as natural, recreational in the fullest sense of the word. The concept of a "prairie," after all, has acquired special meaning for American society, with cultural and historical connotations quite apart from any scientific definition. What is being recreated are historical and cultural environments as much as presumed natural scenes. For those of us who are pyromantics, perhaps the most satisfying outcome is that new visitors to these sites, like the early explorers, will again have the privilege of witnessing one of the great spectacles of the New World - the conflagrating prairie.

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FIRE EFFECTS ON TALLGRASS PRAIRIE

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Abstract. Fire has been an important natural part of tallgrass prairie ecosystems, started by both lightning and American Indians. Production of vegetation on burned areas can be double that on unburned, unmowed, and ungrazed areas where the old standing dead vegetation is deep. Burning stimulates earlier plant development than on unburned areas. In tallgrass prairie, burning stimulates flowering of warm-season grasses and increases stem density. Late spring burning results in fewer forbs but greater grass production than fall or early spring burning. Up to at least six years, above-ground biomass is positively related to the number of years between burning. In Kansas, at least, burning is effective in keeping out exotic plants where the prairie grasses are vigorous.

The few studies of fire effects consistently indicate that neither the ash left from burning nor heat from fires affects production. Warming of the increased growth resulting from burning. The increased light for new growth by removal of the old plants seems to be more important.

INTRODUCTION

This paper reviews fire effects in tallgrass or true prairie of North America, but does not cover effects in mixed or shortgrass grasslands, in which effects of fire may differ from effects in tallgrass prairie.

Lightning is an important cause of fires (Bragg 1982). Records compiled by Westover (1977 through 1984) show that 7.8% of the rural vegetation fires in all of Nebraska for the years 1976 through 1983 were caused by lightning, and these fires burned 25.8% of the area burned by all causes. Lightning has caused fires in many forests and grasslands (for example, see Komarek 1968), and has been a major influence in tallgrass prairie throughout its development. After the arrival of American Indians, fires started by them were added to those started by lightning. We do not know how often prairie areas were burned prior to European settlement. Because of the rate at which forest invades unburned tallgrass prairie (Bragg and Hulbert 1976), we infer that fires must have occurred more than once a decade, perhaps several times a decade.

Controlled experimental burning in native tallgrass prairie (not reestablished prairie) has been rare, so most of our information has been obtained from studies initiated following wild fires. The oldest experimental fire study is on the Aldous experimental plots, located on Kansas State University land close to Manhattan, Kansas. These 10 by 20 m plots have been burned every year since 1928 except eight: one of the rare and highly valuable long-term studies. Aldous plot treatments include: unburned, burned in December, early March, early April, and about the first of May; each replicated twice and not grazed (Aldous 1934). Another long-term study is the experimental burning of 17.8 ha units of cattle-grazed native tallgrass prairie at Kansas State University started in 1950. Units are burned in early March, early April, and about the first of May, another unit is unburned, and all are grazed from about May 1 to October 1 at a moderate stocking rate (2 ha/animal unit) (Owensby and Anderson 1967). Experimental burning was started on Hayden Prairie, Howard County in northeastern Iowa, in 1954 (Ehrenreich 1959). On Tucker Prairie east of Columbia, Missouri, experimental burning was started in 1958 (Kucera et al. 1963). The most extensive experimental burning was begun in 1972 on Konza Prairie Research Natural Area south of Kansas State University, Manhattan, Kansas. Watershed units in tallgrass prairie are unburned, burned in April at 1, 2, 4, and 10 year intervals, burned at irregular intervals, and burned for 3 consecutive years and then not burned for 3 years, with 4 or more replications each on ungrazed watersheds. (Grazing is scheduled to begin soon on other watersheds, also burned and unburned.) In addition, 25 by 25 m plots are burned in November and March.

Scientific names follow usage in the Flora of the Great Plains (Great Plains Flora Association 1986). Common names are from Anderson and Owensby (1969).

EFFECT OF BURNING ON RATE OF DEVELOPMENT OF PRAIRIE VEGETATION

Removal of the standing dead vegetation by either clipping or burning results in more rapid growth of warm-season grasses in the early part of the growing season than on unburned areas (Ehrenreich and Aikman 1963). In 1966, in plots burned April 9 the leaf blades of big bluestem (*Andropogon gerardi*) were 10 to 15 cm tall and fully expanded on May 12, whereas on unburned plots the blades had only grown 2 to 4 cm and were still in the coleoptiles (Hulbert 1969). On Konza Prairie it has been observed that development starts earlier on plots burned in November than on those burned in March, and earlier on March than on May 1 burned plots. Part of the reason for the earlier growth on burned than unburned areas is believed to be a result of higher soil temperatures on burned areas, resulting from greater solar heating as a response to removal of the insulating layer of standing dead vegetation (Aldous 1934, Hulbert 1969, Rice and Parenti 1978).

EFFECT OF BURNING ON PRODUCTIVITY OF VEGETATION

The effect of burning on productivity depends on soil type, frequency of burning, season of burning, weather conditions, and other factors. The difference in productivity is greater on deep, nonrocky loam soils than on shallow, rocky soils. Ungrazed, unmowed, and unburned prairies have distinctly lower yields of vegetation than burned prairies (Table 1). Apparently, an important reason for this effect of fire is the removal of old growth of vegetation, because mowing and removal of dead vegetation results in production similar to that in burned plots (Old 1969, Hulbert 1969, and Rice and Parenti 1978). The earlier an area is burned (i.e., the longer the period between burning and resumption of growth) the lower the production. This has been attributed to lower amounts of water storage in plots burned early than those burned later, due at least in part to greater runoff and therefore less infiltration during the period between burning and the beginning of growth of the vegetation (Anderson 1965).

TABLE 1. Production of aboveground biomass on ungrazed, unmowed, and unburned prairie as a percent of that on adjacent burned prairie.

Location	Yield of unburned prairie as percent of burned	Reference
Oklahoma	60	Rice and Parenti 1978
Oklahoma	64	Adams and Anderson 1978
Kansas	53	Hulbert 1969
Missouri	46	Kucera and Ehrenreich 1962
Iowa	77	Ehrenreich and Aidman 1963
No. Illinois	30	Hadley and Kieckhefer 1963
No. Illinois	65	Old 1969
So. Illinois	50	Anderson and Van Valkenburg 1977

EFFECT OF BURNING ON PLANT REPRODUCTION

Burning stimulates flowering of at least most warm-season grasses. The concept obtained from explorers and early settlers that one needed to be on a horse to see over the grass is misleading, if one assumes that this means the prairie is always that tall. It is true that flower stalks of big bluestem and indiangrass (*Sorghastrum nutans*) can reach 2 to 3 m., but that occurs only on deep loam soil after spring burning and in years with adequate precipitation during the growing season. On Konza Prairie during the 13 years from 1972 through 1984, big bluestem seed stalks grew 2.6 m tall only in 1973 and 1981. Flowering and seed production is particularly good in wet years that follow dry years, a combination that occurred in 1980-81. In September, 1981, as a result, there were stretches of mowed fireguards where one saw only two walls of grass. In contrast, there may be almost no flower stalks in dry years.

The density of flower stalks commonly is increased by burning. In Wisconsin big bluestem flower stalk density was 7 times greater on burned than on unburned plots in the reestablished Curtis Prairie (Curtis and Partch 1950); in Iowa burned plots had 2 to 10 times as many flower stalks of big bluestem, little bluestem (*Andropogon scoparius*), indiangrass and prairie dropseed (*Sporobolus heterolepis*) as unburned plots (Ehrenreich and Aikman 1963); and in Missouri the increase was 2.7 times for big bluestem, 12 times for little bluestem, and 4 times for indiangrass (Kucera and Ehrenreich 1962). Anderson and Van Valkenburg (1977) found little difference in flower culm density of grasses on burned and unburned plots, but the burning occurred in December, a time that is less favorable for stimulating flower stalk production than spring burning (Anderson and Van Valkenburg 1977). However, legumes increased dramatically in response to this fall burning.

Flowering of many species is reduced by spring burning. Both leaf production and flowering of Kentucky bluegrass (*Poa pratensis*) are reduced by burning (Ehrenreich and Aikman 1963, Towne and Owensby 1984). Other cool-season species generally respond in the same way, especially when the fires are in late spring. On Konza Prairie heath aster (*Aster ericoides*) commonly does not flower on areas burned that spring, in contrast to abundant flowering on areas not burned. The response to fire varies, of course, among the hundreds of forbs in prairie.

EFFECT OF BURNING ON WOODY PLANTS

The cause of the "treelessness on the prairies" has been much debated since the beginning of settlement of the prairies (Gaskill 1906, Shimek 1948). Fire and poor drainage were emphasized first, but later other explanations gained proponents, including insufficient rainfall, type of soil, drying winds, geologic formations, and overgrazing by bison. Shimek felt that fire was a minor cause, and emphasized the drying power of the air and the low soil moisture as basic causes of prairie. He disagreed with Gleason (1913) who emphasized the importance of fire as a cause of the lack of trees in prairies.

These disagreements resulted partly from insufficient evidence. Shimek used the observation that trees had not invaded prairie in Iowa since settlement as evident that fire is not a major cause of treelessness (Shimek 1911). Observations over a longer time have corrected that interpretation, especially where tree seed sources were nearby. Another reason for the disagreements was the human tendency to emphasize single causes. It is now clear that fire is necessary to keep woody plants from replacing tallgrass prairie, but fire alone does not make prairie. It is the combination of fire, climate, substrate, and topography that accounts for prairie (Bell and Hulbert 1974).

Forest or woodland invades even the driest part of the tallgrass prairie area when it is left unburned for several decades. In the Flint Hills of Kansas, redcedar (*Juniperus virginiana*) is an especially successful invader of unburned tallgrass prairie (Owensby et al. 1973), along with other species (Towne and Owensby 1984). Comparison of the area occupied by forest at the time of settlement, as recorded in the 1856 Land Office Survey, with area occupied by forest in the 1970's showed that on frequently burned prairies woody plants occupied about the same area today as over a century ago, but on areas not burned for 20 years or longer, forest had invaded, frequently on half or more of the area (Bragg and Hulbert 1976).

Although the season of burning affects the results, most species of woody plants are reduced by most fires (Adams et al. 1982). Autumn burning appeared to be more effective than spring burning in Iowa (Landers 1976, personal communication). Studies in the Flint Hills of Kansas involve spring burning. Late spring burning is particularly helpful in reducing such species as buckbrush or coralberry (*Symphoricarpos orbiculatus*), because it produces leaves prior to late spring fires, and so is hurt when its carbohydrate reserves are low. Smooth sumac (*Rhus glabra*) in contrast, is less affected because new leaves are produced after warm-season grasses have begun to grow, when burning is less likely. Although burning kills the tops of sumac, stem density may increase in response to burning (Adams et al. 1982). However, the amount of sumac on burned and grazed range was less than on unburned in a Kansas study (Owensby and Smith 1973).

EFFECT OF FREQUENCY OF BURNING

Almost all experimental burning has compared annual burning with no burning; the effect of fire frequency has generally been neglected. Kucera and Koelling (1964) report that annual burning of Tucker Prairie in Missouri resulted in a uniform grass cover with a marked reduction in forbs compared to unburned areas. Burning every other year resulted in a greater number of forbs, and burning at 5-year intervals differed little from unburned.

On Konza Prairie Research Natural Area near Manhattan, Kansas, six burning treatments: unburned, burned at 1, 2, 4, and 10 year intervals, and burned irregularly (after each year with more than 1.2 times the median precipitation) were started in 1972 on watershed units. An early finding was that the interval between fires does affect productivity. On ungrazed areas that had not been burned for several years, flower stalks of big bluestem and indiangrass in the first growing season after burning were taller and denser than on sites burned annually. In the first growing season after burning, denser and taller flower stalks resulted from burning every two years than from annual burning, and burning after 6 years resulted in denser and taller stalks than after 2 years (Hulbert and Wilson 1983). Total aboveground biomass showed the same trend, but the difference was less than for flower stalk yield. At present we can only speculate on the cause, which may be related to nutrient supply. It is too early to recommend any particular frequency of burning.

Indiangrass responds distinctly differently than big bluestem to fire interval. Big bluestem in the Kansas Flint Hills is dominant regardless of burning frequency. On ungrazed areas, however, indiangrass declines rapidly as the length of time since burning increases (Fig. 1) (Towne and Owensby 1984, Hulbert and Wilson 1983). Differences in response of the two species are less on shallow than on deep soils, perhaps because of less standing dead on shallow soils. If the amount of standing dead is an important factor, burning would then make less difference to indiangrass than on deep soils.

Burning favors tall warm-season grasses. Perhaps because this makes them more competitive with other species, the number of species is lowest with annual late-spring burning and increases with increasing intervals between fires (Fig. 2).

EFFECT OF SEASON OF BURNING

If a prairie is ungrazed or lightly grazed and not burned recently, there will be enough dead material so that fires can occur any month of the year (Bragg 1982). Lightning fires probably are most

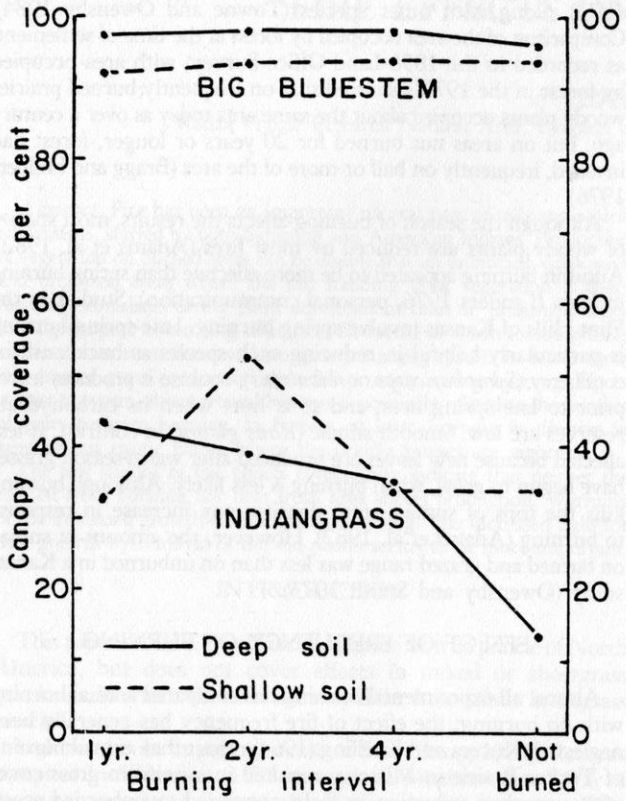

FIG. 1. Effect of frequency of burning on canopy coverage of big bluestem (*Andropogon gerardii*) and indiangrass (*Sorghastrum nutans*) on deep (Tully silty clay loam) and shallow, rocky (Florence cherty silt loam or silty clay loam) soils on Konza Prairie Research Natural Area in Kansas in 1983. Because canopies overlap, the combined totals regularly exceed 100%. Burning was in April each year.

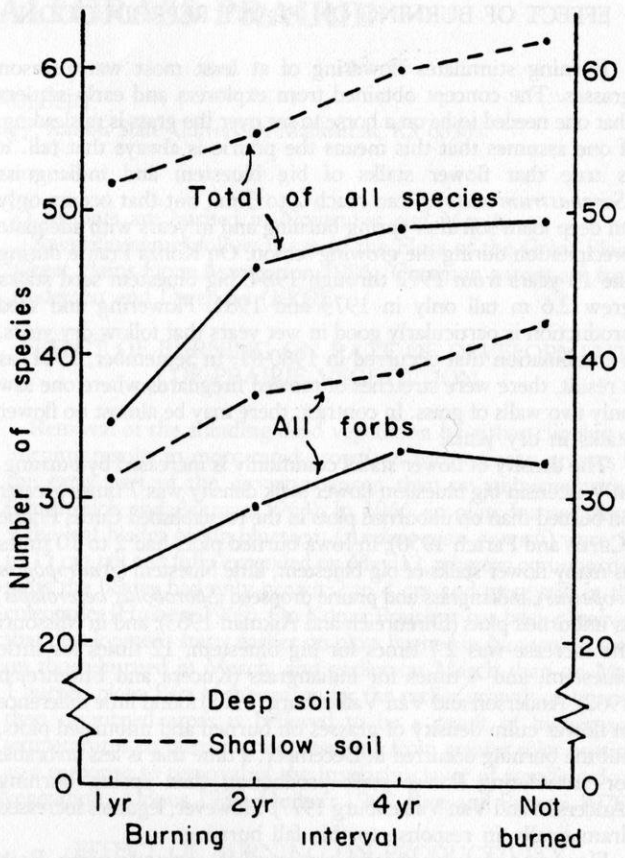

FIG. 2. Effect of frequency of burning and soil depth on number of species in tallgrass prairie on Konza Prairie in 1983.

common in late summer (Bragg 1982). The little evidence indicates that late summer fires reduce productivity. In plots burned in August, 1983, on Konza Prairie, canopy coverage of the grasses was markedly reduced the following growing season.

Burning in late spring (when warm-season grasses have grown 1 to 3 cm) results in greater production but fewer species than earlier burning. On the Aldous plots in Kansas, burned annually at different seasons for 49 of the last 57 years, production was lowest in the December and March burns, intermediate in the April burn, and highest in the May 1 burned plots. There was a larger difference in the grass production than in total production (Towne and Owensby 1984).

On pastures grazed by cattle from May 1 to October 1 and burned about March 10, April 10, or May 1, a similar response was observed. Grass production was about 75% in the March and 90% in the April burned pastures as in the May 1 burned pastures (Owensby and Anderson 1967).

Composition also is affected by season of burning. On Konza Prairie it was found that May 1 burning was better than earlier burning dates for big bluestem and indiangrass, but was less favorable for many other species of grasses and forbs. The greatest number of species was found in the areas burned in March (Fig. 3). Pitcher sage (*Salvia pitcheri*) was most abundant in the late spring burned areas, but most forbs were more common in areas burned in winter or early spring than in those burned in late spring on Konza Prairie and also in the Aldous plots in Kansas (Towne and Owensby 1984).

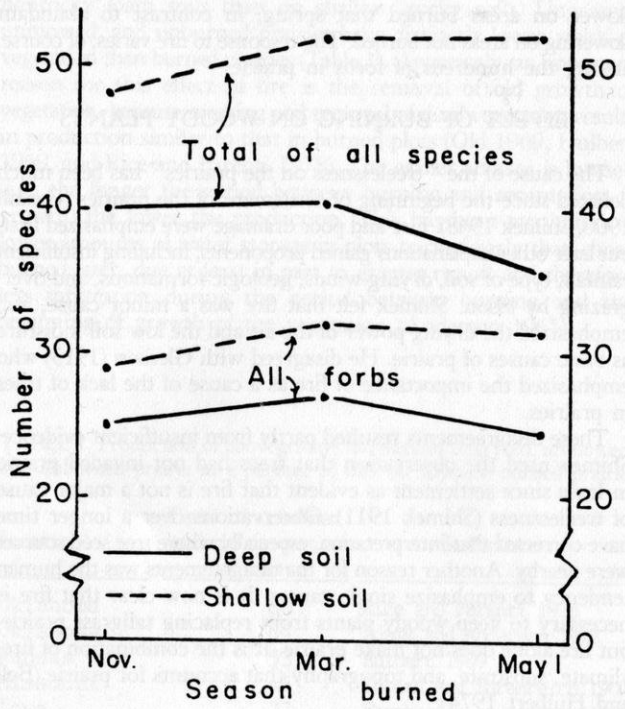

FIG. 3. Effect of season of burning and soil depth on number of species in tallgrass prairie on Konza Prairie in 1983.

EFFECT OF BURNING ON STEM DENSITY

Indiangrass and little bluestem produce distinctly more tillers or stems per unit area on burned than on unburned prairie. Burning has much less effect on stem density of big bluestem, but it shows some increase in stem density with burning. Cool season species, such as Kentucky bluegrass and sedges, produce more stems on unburned sites than on spring-burned areas (Dokken and Hulbert 1978, Towne and Owensby 1984). When the boundary of an annually burned area on Konza Prairie was extended into an area unburned for a decade or longer, there was a strong visual difference in stem density shortly after burning; the area that had been burned annually for several years being much greener for about two weeks because of the denser tillers. In Missouri, Kucera and Koelling (1964) also report greater basal area of grasses on burned than on unburned prairie.

OTHER EFFECTS OF BURNING

Geographical Location

Because climate, substrate, and topography vary throughout the tallgrass prairie area, the response to fire varies. One should not assume that results in one part of the region will apply to another part, but some results do seem to apply throughout. For example, burning seems to favor tall warm-season grasses in all parts of the tallgrass prairie area. On the other hand, the southern part of the tallgrass region, such as the Flint Hills of Kansas, has relatively few cool-season species, whereas the northern portion, in the Dakotas and Manitoba, has a large component of cool-season species. Such differences indicate the need for caution in extrapolating results from one area to another.

Direction of Fire in Relation to the Wind

Fires burning against the wind (back fires) move much slower and produce much lower flames than fires burning with the wind (head fires). As a result, tall woody plants are harmed more by fire with the wind, but the soil is heated less than by fires against the wind. On Konza Prairie we can readily tell whether an area had burned with or against the wind, because ash on the area burned with the wind is black (indicating incomplete fuel consumption), but that burned against the wind is much grayer. Because of this difference we have established four 25 by 25 m plots, two of which are spring burned with the wind, and two against the wind. Species composition was analyzed on two plots burned for 9 years. A statistically significant difference in coverage was found for only one uncommon species. Apparently direction of the fire is unimportant on annually burned areas.

Introduced Plants

Kentucky bluegrass, smooth bromegrass (*Bromus inermis*), sweetclovers (*Melilotus* spp.), and other plants have invaded tallgrass prairie in certain places. Research on these species has been scarce. In the Flint Hills of Kansas where burning has been a regular practice, alien plants are rare except where the native tallgrasses have become weak or absent due to disturbance. Frequent fire eliminates Kentucky bluegrass where the native warm-season grasses are vigorous, but without fire Kentucky bluegrass increases, especially when the area is grazed. Unplowed tallgrass prairie that is grazed but not burned becomes dominated by Kentucky bluegrass from northern Kansas on to the north and east. Often grazed and unburned prairie areas have not been recognized as remnants of tallgrass prairie because of the dominance of bluegrass and weedy forbs. After grazing was reduced and burning initiated, some of these areas have shown remarkable recovery because the native warm-season plants were still present and the fire favored them but hurt the cool-season and weedy species.

On Konza Prairie, yellow sweetclover (*Melilotus officinalis*) entered an annually summer mowed and hayed strip on the south boundary and became dominant some years, yet on the adjacent area, burned annually in April, it is essentially absent. However, it also has entered and become common on a plot burned in November each year.

When Konza Prairie was acquired musk thistle (*Carduus nutans*) was present in heavily grazed spots. Observations indicated that burning favored seedling establishment of musk thistle in areas where grazing had reduced vigor of prairie grasses. However, where the native prairie plants were vigorous, it has been crowded out, whether burned or not. In most cases it appears that the combination of vigorous native prairie plants and frequent burning prevents invasions by exotic plants.

Belowground Effects of Fire

Few people have studied the belowground portion of prairies, and even fewer have compared belowground production on burned and unburned areas. Old (1969) found no difference in root and rhizome weights of plants in burned and unburned prairie in Illinois, but because of the small sample size, differences present may not have been detected. Kucera and Dahlman (1968) in Missouri found 39% less root and rhizome biomass in prairie unburned for 6 years than in prairie burned annually for 10 years. A reduction in belowground biomass is expected to accompany the reduction in aboveground biomass.

Studies on the effects of fire on nutrient supply, soil structure, and soil flora and fauna are much needed. With half or more of the prairie belowground, the importance of understanding what happens there as a result of fire should be obvious.

WHY DOES FIRE AFFECT PRAIRIE?

Effects of fire have been discussed above, but mostly we do not know why they occur. Because fires differ greatly in speed and intensity due to variation in humidity, temperature, wind speed, moisture content, amount of fuel, and predicting effects of a particular fire is difficult. Understanding why fires cause the various effects would much improve our ability to predict.

Hypothesis proposed to account for fire effects on prairie are: loss of nutrients in smoke, increase in the readily available nutrient supply in ash, increase in soil temperature from solar heating after burning, increased light intensity on leaves near the ground due to removal of standing dead plants, and removal of toxicity from dead plants (allelopathy).

Nutrient Changes Due to Burning

Studies on the effect of ash have all yielded negative results. Three studies in tallgrass prairie and one in grassland in England (Lloyd 1972) have detected no effect of the ash in the growing season subsequent to burning. In a study in Kansas, dead vegetation was clipped and then burned in a metal pan. The ash then was returned to the plot. No difference in aboveground yield was detected between this treatment and clipped plots with no ash (Hulbert 1969). In a later study in Kansas, three times as much ash was added to clipped plots as would result from normal burning, yet again no difference from clipped plots without ash was detected (Manuscript in preparation). In Illinois, Old (1969) did a similar study, also with no yield differences detected. It is difficult to accept the idea that leaving nutrients in ash is not important, but it may be that nutrients used the year after burning come primarily from sources already in the soil rather than from ash at the surface. Also, it seems reasonable that the nutrients in ash are less important than nitrogen, which is nearly absent in ash. Studies of soil chemistry on areas long burned show some differences from unburned areas, although the differences were not thought to be important to productivity (Owensby and Wyrill 1973).

Allelopathy

Elroy Rice, a specialist in allelopathy, conducted an experiment in Oklahoma to see if standing dead plants produced chemicals that inhibited new growth of prairie plants. The results indicated that no such inhibition was present (Rice and Parenti 1978). Thus, the present evidence does not support the hypothesis that removal of allelopathy accounts for increased prairie production as a result of burning.

Increased Soil Temperature as a Result of Burning

Rice and Parenti (1978) concluded from their study of allelopathy that the increased productivity of burned areas resulted from the warmer temperature of burned than of unburned soils. Soils of burned areas warm distinctly faster than soils of unburned plots, due to removal of the litter and standing dead plants, and perhaps also due to the darker surface resulting from burning (Kelting 1957, Hulbert 1969). To test this hypothesis, water in an insulated tank heated by electric heaters was pumped through small plastic tubes inserted under standing dead plants in unburned plots so the tubes lay on the soil surface. Soil temperature was monitored. The resulting aboveground biomass was significantly greater on the plots unburned and warmed than on those unburned and not warmed. However, the increase in production was much less than that on burned plots, so it appears that soil warming is only a minor part of the reason for the increased production resulting from burning. It seems highly probable that increased light intensity for early growth resulting from the removal of standing dead vegetation is an important factor (Manuscript in preparation).

ACKNOWLEDGEMENTS

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VEGETATION RESPONSES TO SPRING BURNING IN WESTERN SOUTH DAKOTA

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Abstract. Responses of a Mixed Prairie community to spring burning in 1976 were monitored for two growing seasons. Total vegetation yields on the burn were significantly less than those on the unburned area in both the first and second growing seasons postburn.

In the first postburn growing season yields of bluegrasses (*Poa* spp.) and green needlegrass (*Stipa viridula*) were significantly lower on the burned area than those on the unburned area. In contrast, yields of western wheatgrass (*Agropyron smithii*), needleandthread (*S. comata*), and shortgrasses were significantly greater on the burned area. Similar relationships were recorded in the second postburn growing season, except that needleandthread yields were greatest on the unburned area. Western wheatgrass density after burning was significantly increased while its height significantly decreased. Responses of this species to spring burning corroborated results of earlier studies. The net effect of spring burning in a plant community dominated by cool-season grasses was a measurable improvement in range condition.

INTRODUCTION

Fires were almost an annual occurrence over much of the eastern Tallgrass Prairie region before settlement (Humphrey 1962). In the drier plains west of the 100th meridian the occurrence of fires was not recorded as often, although they were still a characteristic feature of the landscape. Lower precipitation and more frequent droughts provided less fuel for fires in the drier plains, according to Humphrey (1962). Yet, reports of some early explorers to the region mentioned the large extent, ferocity, and beauty of grassland fires (Ludlow 1875, Dodge 1876).

The frequency and extent of rather recent lightning fires in selected areas of the western Dakotas strongly suggest that fire favored grasslands over woodlands (Higgins 1984). Lightning and cultural fires in the pre-settlement era probably burned until interrupted by precipitation, cool atmospheric temperatures, natural barriers of streams and wetlands, sparcity of fuels due to grazing of native herbivores, or by significant topographic barriers, according to Higgins (1984).

Prescribed burning, commonly used as a management tool in the Flint Hills of Kansas, has not become an accepted practice further west and north in either the Shortgrass Plains or the Mixed Prairie. Studies of the effects of wildfires on vegetation in western Kansas have indicated that fire can be detrimental. Hopkins et al. (1948) reported sizeable yield reductions of blue grama(*Bouteloua gracilis*) in the first season following a wildfire. A study of a March wildfire in western Kansas concluded that yields of all species [including buffalograss (*Buchloe dactyloides*), blue grama, and western wheatgrass (*Agropyron smithii*)] were reduced for two seasons following the fire (Launchbaugh 1964). Herbaceous production of Mixed Prairie grassland in western North Dakota was also reduced by a mid-August wildfire (Dix 1960). Fires during the growing season appear to be detrimental to most, if not all, plants. According to Wright (1974), fires during dry seasons or dry years may be harmful because they intensify the drought stress on plants.

This study was conducted in a western wheatgrass-needleandthread (*Stipa comata*) plant community to evaluate the effect of prescribed burning in spring on the vegetation components. The study was conducted in cooperation with personnel of Wind Cave National Park.

STUDY AREA

Wind Cave National Park is a 11,355 ha (28,059 ac) tract of Mixed Prairie and ponderosa pine (*Pinus ponderosa*) forest located in the southeastern foothills of the Black Hills in western South Dakota (U.S. Dep. of the Interior 1973). Fire suppression, combined with light to moderate grazing by wildlife, has resulted in the accumulation of large amounts of herbaceous fuel. One objective of the prescribed burning program in the Park was to reduce wildfire conflagration hazards which exist because of excessive fuel accumulations (Shilts 1976).

The study area was located on a nearly level bench in the southwest corner of the Park. Average annual precipitation in the Park is about 422 mm (16.6 in), 78 percent of which normally occurs between April 1 and September 30 (from Wind Cave N.P. weather records, 1952-83). Soils of the study area were deep, dark-reddish colored silt loams derived from underlying gypsiferous red shales, either weathered in place or transported by wind and water (U.S. Dep. Agri. 1969). Silty clay subsoil layers were calcareous at about 38 cm (15 in). Slopes were gentle, 2 to 6 percent, but increased to 25 percent or more at the north edge where grassland changed to a shrub community.

METHODS

About 6 to 8 ha (10-20 ac) of Mixed Prairie grassland were burned on April 21, 1976. The only predetermined conditions for the burn were relative humidity of 45 percent or less, steady winds of 19 to 24 km/h (12-15 mph), with gusts under 32 km/h (20 mph). Because of shifting winds just before ignition, most of the area was burned with a strip-headfire and flank fire. At ignition, winds were southeast 13 to 19 km/h (8-12 mph), temperature 20° C (70° F), and relative humidity was 40 percent.

Since the area was subject to grazing by native herbivores, portable wire exclosures (cages) were used to protect small areas for sampling vegetation. Three rows of five cages per row were randomly placed perpendicular to the slope on both the burned and unburned areas. Cages were relocated prior to the 1977 growing season.

Vegetation yields were sampled in August 1976 and July 1977 on the burn and in the adjacent, unburned area at elevations of 1,213 to 1,219 m (3,980-4,000 ft). The current year's growth was clipped to ground level in 0.61 x 1.46 m (2 x 4.8 ft) plots within the wire cages in 1976. The same sampling technique was used in 1977, except the size of the sampling unit was reduced to 0.30 x 1.46 m (1 x 4.8 ft). Vegetation was separated into nine components: western wheatgrass, needleandthread, green needlegrass (*Stipa viridula*), bluegrasses (*Poa* spp.), shortgrasses (*Bouteloua* spp.), other grasses and sedges (*Carex* spp.), forbs, and shrubs. Samples were oven-dried at 70°C for 24 hours and weighed to the nearest 0.1 gram.

Maximum needleandthread leaf height (culms without seedstalks) was sampled in late summer 1976. Fifty plants were randomly selected from outside the cages on the burned area. In late June 1977, leaf heights of 100 ungrazed western wheatgrass plants in each treatment were measured. In mid-July, density of that species

TABLE 1. Comparison of mean vegetation yields (gm/m²) and composition (%) on burned and unburned Mixed Prairie, Wind Cave Canyon, Wind Cave National Park, burned April 21, 1976.

	1976				1977			
	BURNED		UNBURNED		BURNED		UNBURNED	
Vegetation Components	Yield	Comp.	Yield	Comp.	Yield	Comp.	Yield	Comp.
Western wheatgrass	17.5*	10.8	6.2	3.5	13.5*	15.4	4.3	3.9
Needleandthread	91.2*	56.4	60.9	34.3	32.9*	37.7	54.4	48.6
Green needlegrass	0.1*	0.1	7.5	4.2	0.7	0.8	7.7	6.9
Bluegrasses	1.5*	1.0	45.7	25.8	2.4*	2.8	19.1	17.1
Shortgrasses	15.9*	9.8	2.9	1.6	11.6*	13.3	2.6	2.3
Other grasses & sedges	11.4	7.0	11.0	6.2	4.3	4.9	10.0	8.9
Forbs	23.8	14.7	42.9	24.2	12.6	14.4	13.7	12.3
Shrubs	0.4	0.2	0.4	0.2	9.3	10.7	0.0	0.0
TOTALS	161.8*	100.0	177.5	100.0	87.3*	100.0	111.8	100.0

* Treatment was significantly different from the control ($P \leq 0.10$); gm/m^2 x 8.9236 = lb/ac.

was estimated using a 0.30 x 0.30 m (1 x 1 ft) frame randomly placed along transects located by restricted randomization. Stem counts were made in 50 frames per treatment.

Standard analysis of variance using a nested design (treatment and rows of samples within treatments) was used to analyze vegetation yield data. Analyses were made using a least squares method (Harvey 1975). Treatment means were compared to control means and significance at the 90 percent confidence level was determined by the F-ratio test. Comparisons of the western wheatgrass height and density data were made at the 90 percent confidence level using Student's t-test.

RESULTS AND DISCUSSION

Annual precipitation in Wind Cave National Park in 1976 and 1977 was 63 and 30 mm (2.5 and 1.2 in), respectively, above the 31-year average. However, precipitation in the nine months preceding the burn (July 1975 through March 1976) was 50 mm (2 in) below average. In April 1976, precipitation was 58 mm (2.3 in) above the monthly average (44 mm), with approximately 50 percent occurring after the burn. Postburn precipitation in May 1976 was slightly below average (Fig. 1). A cool-season precipitation deficit occurred during the period September 1976 through June 1977 (Fig. 1). Responses of cool-season native grasses to the late April burn may have been more positive if cool-season precipitation had been average or above.

Yields of nearly all vegetation components were considerably lower in 1977 than in 1976, irrespective of treatment (Table 1). Total vegetation yields on the burned area in both 1976 and 1977 were significantly lower than those on the unburned area. Several factors, in addition to precipitation deficits, could have contributed to suppressed yields on the burned area. Launchbaugh (1973) reported that removal of mulch by mowing and raking or by burning resulted in greater plant exposure to cold winter temperatures, increased use of stored carbohydrates through respiration during dormant seasons, and less favorable soil moisture relations than were found in unburned areas. Because of dry conditions prior to the late April burn, mulch was almost completely consumed by the fire, leaving soils exposed to greater wind, solar radiation, and evaporation.

Total yields on the burned area were only nine percent lower than those on the unburned area in 1976, but in 1977 that difference more than doubled to 22 percent (Table 1). Destruction of the mulch component by burning and the postburn precipitation deficit were probably key factors relating to this difference.

Soils on burned areas warm earlier in spring due to greater absorption of solar radiation. According to Daubenmire (1968), warmed soils lower water viscosity and, in turn, speed up percolation and lower the amount of available soil water at field capacity. Thus, water available for plant use is decreased. These influences, coupled with increased evaporation from a denuded and warmed surface, may have enhanced drought and resulted in reduced yields of total vegetation.

The spring burn and postburn weather apparently were timely for improving vigor of needleandthread and western wheatgrass. Yields of both species were significantly greater on the burned area than on the unburned area in the first growing season after burning (Table 1). Green needlegrass yields appear to have been reduced by burning, but that species comprised less than five percent of the total vegetation in 1976, and only about seven percent in 1977. In the second postburn growing season western wheatgrass yields were also greater while needleandthread yields were significantly lower on the burn compared with the unburned area.

A stimulation of flowering (inflorescence size and number) of needleandthread was observed on the burned area the first postburn growing season and may have contributed to the yield increase for that species. Other researchers have reported that flowering of tallgrass species was stimulated by burning (Curtis and Partch 1950, Probasco and Bjugstad 1977). Dix (1960) reported a decrease in flowering of needleandthread in North Dakota after late May, August, and September burns. Burning in early spring at Wind Cave apparently resulted in little, if any, damage to needleandthread, and the additional flowering culms contributed to its relatively high yield in 1976.

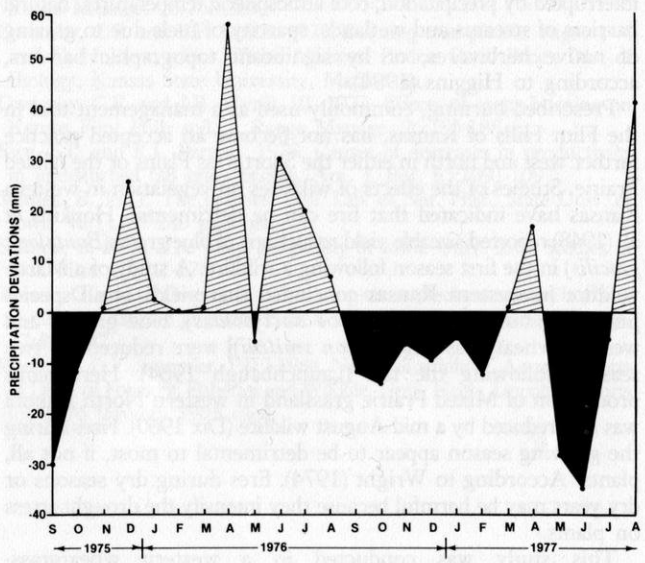

FIG. 1. Deviations in monthly precipitation (mm), September 1975 through August 1977, at Wind Cave National Park, calculated from 31-year record, 1953-1983.

Grazing of regrowth vegetation on a burned area results in further plant stress, especially when plants are grazed too soon after growth is initiated. The degree of stress is compounded when soil moisture is deficient. While large numbers of bison did not normally frequent the study area, lone bulls or small groups of bulls utilized the area and were especially attracted to regrowth on the burn in 1976. Plant height measures revealed the preference of bison for regrowth on the burn. Maximum leaf heights of needleandthread were significantly greater ($P \leq 0.10$) on the unburned area (30.2 cm) than either inside cages (22.4 cm) or outside cages (20.5 cm) on the burn. The fall 1976 and winter 1977 precipitation deficit (Fig. 1) probably further stressed needleandthread, and the combined effects undoubtedly led to greatly reduced yields in 1977 on the burned area.

Livestock management is important on burned areas. Ungulates, native or domestic, will concentrate on burned areas because the regrowth vegetation is more palatable, nutritious, and devoid of old growth (Smith et al. 1960, Smith and Owensby 1973, Barker and Erickson 1974, Vogl 1974, Gartner 1975, Gartner et al. 1978). Heavy grazing of burned Mixed Prairie would delay the replacement of mulch and prolong dry soil conditions.

Yield and density of western wheatgrass can be expected to increase on late winter and early spring burns in western South Dakota (Gartner et al. 1978). Yields of this species are generally dependent on cool-season precipitation. Several factors may account for increased vigor of western wheatgrass, especially yield increases, after burning. Rhizomatous species may be stimulated by burning to the extent that new shoots are initiated from each rhizome. According to Vogl (1974), vegetative reproduction is advantageous and helps species survive fire. He stated: "Environmental extremes common to many grasslands, including those created by fire, were probably selective forces in favoring perennials with vegetative habits."

Rhizome reproduction is reliable in dry conditions because the established root systems of the mother plant provide water and energy for new shoots. Thus, rhizomatous plants have a competitive advantage over seedlings (Vogl 1974, Stoddart et al. 1975). Rhizomatous plants can also take advantage of space as soon as openings are created. Albertson and Weaver (1944) reported western wheatgrass rhizomes extended into bare soil created by the reduction of tallgrass species as a result of severe drought. Removal of mulch by burning may create a drier surface soil, resulting in a poor microclimate for seed reproduction. Decreases in other vegetative components would also create growing space for rhizomatous species.

The late April burn resulted in an increase in western wheatgrass density and a decrease in height even into the second growing season after the burn (Fig. 2). Differences in both parameters between burned and unburned areas were significant ($P \leq 0.10$). Western wheatgrass yield increases on the burned area can probably be attributed to increased density. Similar height and density relationships were recorded in other western South Dakota studies (Gartner 1975, Gartner et al. 1978).

Bluegrass yields were significantly reduced in both the first and second growing seasons after burning (Table 1). Spring burning, after cool-season species such as bluegrasses and sedges initiate growth, retards further growth (McMurphy and Anderson 1965, Anderson et al. 1970, Smith and Owensby 1973). This practice has been effective for reducing the abundance of Kentucky bluegrass in native grasslands (Smith and Owensby 1973).

Increased yields of shortgrasses (Table 1) may have been the result of reduced competition from some of the cool-season species (bluegrasses and sedges) coupled with above-average warm-season precipitation in 1976. Earlier soil warming on the burned area may have induced earlier growth of warm-season shortgrasses, further contributing to their yield increases.

Forbs appear to have been reduced by burning in the first postburn growing season even though the difference in forb yields between the burned and unburned areas was not statistically

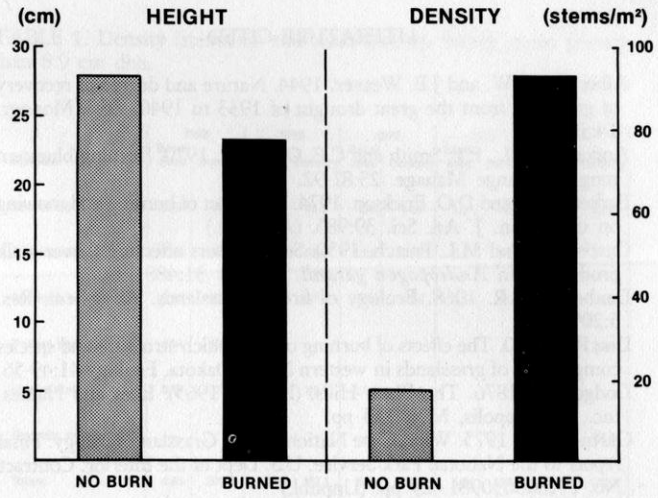

FIG. 2. Mean leaf height and density of western wheatgrass in a burned and unburned Mixed Prairie community in Wind Cave National Park, sampled in second growing season after burning.

significant. Photographs taken before vegetation samples were clipped reveal that scurfpeas (*Psoralea* spp.) and sageworts (*Artemisia* spp.) were quite common in the burn.

SUMMARY AND CONCLUSIONS

Prescribed burning in spring resulted in lower total herbaceous yields in a Mixed Prairie community in western South Dakota. Burning was effective in reducing bluegrasses, primarily the exotic Kentucky bluegrass. Burning increased yields of shortgrasses, probably because of a longer growing season resulting from earlier soil warming on the burned area, reduced competition from some cool-season grasses, and favorable summer precipitation.

Burning effectively increased yields of western wheatgrass, an important species on most western South Dakota range sites. Increasing the density of western wheatgrass would improve range condition on most normal upland range sites in western South Dakota.

Total productivity on both the burned and unburned areas was drastically reduced in the second postburn growing season. Below average precipitation in late 1976 and early 1977 was the major contributing factor. However, the degree of yield reduction was greater on the burned area, probably because of increased bison grazing activity. Grazing probably also affected the rate of mulch replacement on the burn which exposed the soil to greater evaporative forces and may have reduced available soil water.

In summary, burning increased yields of desirable native species (western wheatgrass and shortgrasses) and decreased yields of exotic species (bluegrasses). Vegetation responses to the burn were interpreted to indicate that range condition was improved and, after a period of recovery and average precipitation, total productivity could be expected to improve.

ACKNOWLEDGEMENTS

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EFFECT OF ELEVEN YEARS OF FIRE EXCLUSION ON THE VEGETATION OF A SOUTHERN ILLINOIS BARREN REMNANT

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Abstract. Five permanent plots established in 1968 to monitor the effects of fire on southern Illinois barren vegetation and the invading exotic Japanese honeysuckle (*Lonicera japonica*) were resampled in 1983 after eleven years of fire exclusion. The 1983 data were compared with preburn (1968) and three years of postburn data (1969-1971). Between 1971 and 1983, tree density increased slightly but basal area increased from 5.5 to 7.9 m^2 /ha. Woody plants (tree species and shrubs) $>$ 15.0 cm tall but $\leq$ 8.9 cm dbh were surveyed in five size classes. For the 1983 sample, there were more stems in the third size class, but fewer stems in the largest and smallest classes than in samples taken in previous years. Frequency of prairie forbs and ragweed (*Ambrosia artemisiifolia*) declined after fire exclusion, whereas woodland herbs increased. Percentage similarity of herbaceous flora was calculated between all sample years. The 1983 sample had less similarity to each of the earlier years than the earlier years had to each other, indicating that in the absence of fire, the barren has undergone continuous changes in floral composition and vegetative structure and is succeeding from a barren to a deciduous forest.

INTRODUCTION

In Illinois, barrens are considered local inclusions of prairie flora, mixed with forest, in forested land (Vestal 1936, White and Madany 1978). Barrens were described by early government land surveyors as grassy areas containing more trees and shrubs than occurred in prairie. Some barrens appear to owe their existence to soil and edaphic factors while others seem to have been maintained by frequent fires. Few of the barrens present in Illinois at the time of settlement have survived to the present. This is probably due to destruction for land development and succession to forest on non-agricultural sites once frequent wildfires were stopped after settlement.

During 1968, five permanent quadrats were established in a barren remnant in extreme southern Illinois to study the effect of prescribed burning on barren vegetation and the exotic Japanese honeysuckle (*Lonicera japonica*) that was invading the site (Anderson and Schwegman 1972). The study area is located in a remote part of the Shawnee National Forest and was not visited by either of us from 1972 until 1983. The 1983 visit revealed that a marked shift from herbaceous to shrub and forest vegetation had taken place in the intervening years and the site was resampled to document this change.

Our site is located within the Costal Plain Natural Division of Illinois (Schwegman et al. 1973) and consists of a 0.2 ha opening in the forest on level terrain along the intermittent Burke Branch Creek (SW 1/4 Sect. 4, T15S, R6E, Pope County). The site is 56 km south of the distribution of prairie in Illinois, as mapped by

government land surveys about 1820 (Anderson 1970). The dominant herbaceous plants are the bluestems *Andropogon gerardi* and *Schizachyrium scoparium*, with Indian grass *Sorghastrum nutans* abundant in local areas. A diverse flora including 125 herb species and 26 tree and shrub species is present.

The site was burned in the springs of 1969, 1970, 1972 and 1973. Thus, it had been 11 growing seasons without burning when it was resampled in August of 1983. This paper compares sample data from preburn 1968 and post burn 1969, 1970 and 1971 with the 1983 data from the five permanent sampling plots.

METHODS

All measurements were made in English units that are converted to their metric equivalents in this paper.

Diameters of all trees greater than 8.9 cm dbh were measured in four 1/100 ha and one 1/247 ha permanently marked circular quadrats. Seedlings, saplings and shrubs were sampled in 1/247 ha plots nested within tree quadrats and placed into one of five size classes: (1) > 15.0 cm tall but ≤ 1.4 m tall, (2) > 1.4 m tall but ≤ 1.2 cm dbh, (3) > 1.2 cm but ≤ 3.8 cm dbh, (4) > 3.8 cm but ≤ 6.4 cm dbh, and (5) > 6.4 cm but ≤ 8.9 cm dbh.

Ten one meter square quadrats were nested within the 1/100 ha tree plots to sample herbs and woody plants less than 15.0 cm tall. In the 1/247 hectare tree plot, only four quadrats were located. Japanese honeysuckle was sampled by nesting five decimeter square quadrats within each of the m² quadrats. Sampling was accomplished in late August or September.

RESULTS AND DISCUSSIONS

Tree density increased 14.4% from 157.2 stems/ha in 1971 to 179.5 stems/ha in 1983 (Table 1). Tree basal area increased 43.6%, from 5.5 m² /ha to 7.9 m² /ha, over the same time period. Red cedar (*Juniperus virgiana*), which did not occur on the sampling plots, disappeared from the study area following the first two burns. Loblolly pine (*Pinus taeda*) invaded the site from nearby plantations between 1971 and 1983. Two specimens about 3 m tall, but too small to measure as trees, were conspicuous in the remaining open area in 1983.

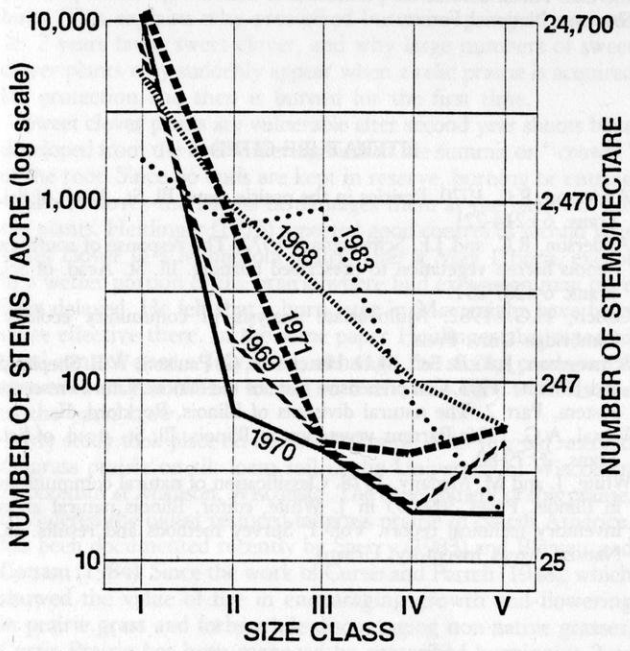

FIG. 1. Change in the number of woody stems by size class.

TABLE 1. Density (stems/ha) and basal area (m /ha) of stems greater than 8.9 cm dbh.

Species	1968 Basal Area	1968 Density	1969 Basal Area	1969 Density	1970 Basal Area	1970 Density	1971 Basal Area	1971 Density	1983 Basal Area	1983 Density
Betula nigra	1.47	44.9	1.44	44.9	1.51	44.9	1.8	44.9	1.4	22.4
Juglans nigra	0.32	44.9	0.16	22.4	0.32	44.9	0.4	44.9	1.2	67.4
Platanus occidentalis	2.84	67.4	2.84	67.4	3.01	67.4	3.3	67.4	3.7	44.9
Prunus serotina	0.14	22.4	—	—	—	—	—		0.2	22.4
Ulmus alata	0.16	22.4	0.16	22.4	0.16	22.4			—	
Quercus muhlenbergii	—		—	—	—				1.4	22.4
Totals	4.93	202.0	4.60	157.1	5.0	179.6	5.5	157.2	7.9	179.5

Tree density did not increase rapidly considering the time length (12 years) between samples. However, increased dominance of the area by trees, as expressed in the more rapid increase in tree basal area than density, was apparent. Two of the plots that were originally established in barrens were, in 1983, completely under a forest canopy. Black walnut (*Juglans nigra*) and sycamore (*Platanus occidentalis*) were the leading dominants in the tree stratum with 67.4 and 44.9 trees/ha, respectively (Table 1).

For woody plants ≤ 8.9 cm dbh, the number of small stems (size class I) and large stems (size class V) were lower in 1983 than at any other sample period during the study. However, the density of medium sized stems (size class III) was greater in 1983 than during any previous sample year (Fig. 1). The lower number of small stems may indicate reduced sprouting in the absence of

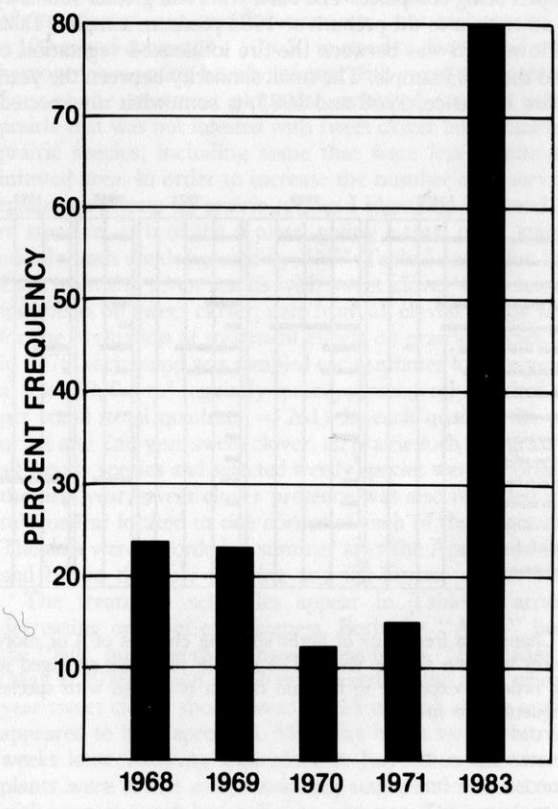

FIG. 2. Frequency of *Lonicera japonica* in 220 10 cm x 10 cm quadrats.

TABLE 2. Percentage similarity of herbaceous flora between all sample years (arranged by decreasing exposure to fire).

	1970	1969	1971	1968	1983
1970	*				
1969	66.4	*			
1971	68.2	71.6	*		
1968	51.3	55.2	56.6	*	
1983	40.7	44.1	39.7	40.7	*

fire and reduced shrub and sapling growth due to shading in plots that were formerly barrens but were, in 1983, under forest canopy. The reduction in size class V saplings may represent a loss of tree reproduction resulting from earlier fire mortality.

Considering density combined across size classes, most woody species decreased in density from 1971 to 1983. Exceptions are two tree species, river birch and slippery elm that increased from 0 to 723 stems/ha and from 433 to 578 stems/ha, respectively. Open habitat shrubs showed the greatest decline in density. Prairie willow (*Salix humilis*) declined from 11,568 stems/ha in 1971 to 2,651 stems/ha in 1983 while dogwood (*Cornus ammomum*) decreased from 3,518 stems/ha to 1,060 stems/ha.

Japanese honeysuckle showed a positive response to fire exclusion and an ability to spread in spite of increasing shade on the plots. This species decreased following the burns (1969 and 1970) but nearly quadrupled its preburn (1968) frequency by 1983 in the absence of fire (Fig. 2).

Frequency data for herbaceous species and woody stems less than 15 cm high were analyzed following Gauch (1982) to determine percentage similarity (PS) between each sample year. The PS is derived from the shared frequency of all species in the two samples being compared. The burn years had greater similarity to each other than to the preburn or 1983 postburn samples (Table 2). The lowest PS was between the fire influenced vegetation of 1971 and the 1983 sample. The small similarity between the years of low fire influence, 1968 and 1983, is somewhat unexpected.

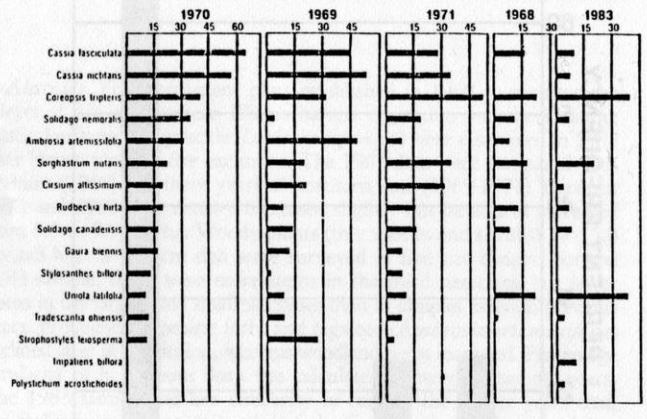

FIG. 3. Changes in frequency of herbs showing changes of 4 or more occurrences between sample years. The sample years are arranged in declining order of exposure to fire and the list is headed with species most frequent after fires.

While both years had a larger number of forest species than the burn years, some of the forest species present in the 1983 sample were different from those in the 1968 sample. Also, the disappearance of and decrease in abundance of some species, as described below, reduced the floristic similarity between the 1968 and 1983 samples.

Varied responses to burning and fire exclusion were found among herbaceous species (Fig. 3). Population levels of the two annual *Cassia* species were highest after the greatest exposure to fire, and both species declined in the absence of fire. A second pattern for an annual herb was expressed by *Ambrosia artemisiifolia* which peaked after the first fire and then declined, with both repeated burning and fire exclusion. Ragweed was not present on the sample plots in 1983 (Fig. 3). Some species, such as *Gaura biennis*, increased with burning but disappeared after 10 years of fire exclusion. On the other hand, woodland herbs such as *Uniola latifolia* decreased with repeated burning but increased between 1971 and 1983. During this same period, new woodland species, such as *Impatiens biflora* and *Polystichum acrostichoides*, appeared.

CONCLUSION

The study area is succeeding from a barren to a forest community in the absence of fire. This succession was modified by the past fire history of the site. During the period of fire exclusion, growth of existing trees was more important in increasing the woodland character of the site than increasing tree density. The slow increase in tree density was due in part to a gap in tree reproduction caused by fire mortality. Medium sized shrubs and tree reproduction, apparently resulting from 11 year old fire-induced sprouts, were more abundant in 1983 than at any time during the study. These plants accounted for the present brushy appearance of the remaining barren. Herbs favored by fire and open habitats declined, while some forest herbs increased and others were invading the area for the first time. Japanese honeysuckle continued to spread throughout the area.

ACKNOWLEDGEMENTS

We wish to thank K. Andrew West for help with field sampling and the U.S. Forest Service for permission to conduct this research on the Shawnee National Forest.

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RESPONSE OF SWEET CLOVER (*MELILOTUS ALBA* DESR.) AND ASSOCIATED PRAIRIE VEGETATION TO SEVEN EXPERIMENTAL BURNING AND MOWING TREATMENTS

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Abstract. Seven experimental treatment plots were subjected to different burning and mowing schedules over a six-year period to determine the procedure most effective in controlling white sweet clover (*Melilotus alba*) in a restored tallgrass prairie in Wisconsin. A minimum of 20 permanent 0.5 m² quadrats were set up in each treatment plot and the species present in each quadrat were recorded each year. The treatments tested included early spring burns at two- and four-year intervals, early spring burns followed the next year either by a May burn or by mowing in July, May burns in three consecutive years, and repeated dormant season (spring and fall) burns. The early spring burn-May burn sequence achieved the best control of sweet clover, while the least successful were the variously timed spring and fall burns. Successful treatments were associated with more reductions in prairie forb frequencies, while dormant season burns tended to increase forb frequencies. Management implications are discussed.

INTRODUCTION

White sweet clover, *Melilotus alba*, is a Eurasian legume which has become a serious pest in midwestern prairies, including both preserved relic prairies and planted restorations. It appears to thrive under the common prairie management practice of occasional spring burns. Heitlinger (1975) and Klemow and Raynal (1981) cite selected literature on sweet clover introduction, its economic value, and species characteristics.

Although annual strains are known, *M. alba* in the study area appears to be an obligate biennial. It has seeds that can remain viable in the soil for decades. Early spring burns trigger germination of the seeds; the plants overwinter and produce seeds the second year, replenishing the seed bank in the soil in advance of the next burn. This explains why prescribed burns in spring at intervals $\geq$ 2 years favor sweet clover, and why large numbers of sweet clover plants may suddenly appear when a relic prairie is acquired for protection and then is burned for the first time.

Sweet clover plants are vulnerable after second year shoots have developed from the overwintering buds at the summit or "crown" of the root. Since no buds are kept in reserve, burning or cutting which removes the shoots or damages them at the base will kill the plants. Heitlinger (1975) reported good control of second year sweet clover in a Minnesota prairie after a May 1 burn, except in a wetter portion of the prairie where bud expansion may have been delayed. He felt that a burn later in May might have been more effective there. In the same paper Heitlinger also reported good control after a July burn, although the smoke produced at that time of year was a hazard to traffic and very troublesome to the burn crew.

My study took place on the Curtis Prairie, a 45 year-old restored tallgrass prairie on silt loam soil in the University of Wisconsin Arboretum at Madison, Wisconsin. The development of this prairie, considered the oldest restored tallgrass prairie in North America, has been documented recently by Sperry (1983) and Blewett and Cottam (1984). Since the work of Curtis and Partch (1948), which showed the value of fire in encouraging growth and flowering in prairie grass and forbs while discouraging non-native grasses, Curtis Prairie has been managed by prescribed burning at 2 or 3 year intervals, usually in early spring. This is a schedule that practically guarantees a buildup of sweet clover. Even in the first study Curtis and Partch noted that the bare ground resulting from destruction of the bluegrass sod was colonized not only by prairie species but also by weedy species. They found extremely high densities of sweet clover in part of a plot burned in March, which "resulted in the nearly complete exclusion of all other plant species."

In 1977 an April burn was carried out in a large central section of Curtis Prairie which was last burned in 1974. It was an excellent, hot burn. Field checks that fall revealed that substantial areas of the prairie contained dense, vigorous first year plants. This cohort overwintered well and in 1978, a year with excellent growing conditions, the second year plants in untreated areas formed a nearly continuous canopy often over 2 m high. The uniformly dense infestation of a diverse section of the restored prairie provided the opportunity to evaluate the response of both sweet clover and prairie species to a variety of treatments.

METHODS

Seven treatment plots were laid out so that each extended into the heavily infested area in the central portion of the prairie. Plot size and shape varied because of the shape of the prairie, shape of the infested area, trail locations, etc., but each was at least 50 x 100 m and contained a 50 x 50 m stand of diverse and reasonably homogeneous prairie heavily infested with sweet clover throughout. Four of the treatment plots also extended across a part of the prairie that was not infested with sweet clover but contained many prairie species, including some that were less common in the infested area. In order to increase the number of observations of treatment effects on prairie species I identified a second 50 x 50 m stand in each of the 4 plots, giving a total of 11 stands. The added stands are designated by "N" (Table 3 and 4) for "north." Data from the seven stands with sweet clover were summarized for effects on sweet clover; data from all eleven stands were used for the evaluation of treatment effects on prairie species. Starting in 1978, each stand was sampled each summer for five years using at least 20, 0.5 m² regularly spaced, permanently marked quadrats per stand (total quadrats = 261). In each quadrat the presence of 1st and 2nd year sweet clover, all prairie forb and grass species, all woody species and selected weedy species were recorded. After the first year, sweet clover presence was also recorded in a 0.02 m² quadrat located in one corner of each of the larger quadrats. The data were recorded in summer after the April and May burns and before the July mowing and fall burns.

The treatment schedules appear in Table 1, arranged in decreasing order of effectiveness. Both the "April" burns and the "fall" burns were dormant season burns. "Early May" burns (May 1, 1978; May 8, 1979) were timed to take place when second year sweet clover shoots were $\geq$ 15 cm and all the crown buds appeared to have sprouted. Mid-May burns were arbitrarily two weeks later. Mowing took place in July when the sweet clover plants were in the early flowering stage, and was accomplished with a rotary brush bull pulled by a tractor. The cut plant material was left in place.

TABLE 1. Treatment schedule.

	1977	1978	1979	1980	1981	1982
EM Early May	April burn	May 1 burn			April burn	May 13 burn
MM Mid-May	April burn	May 15 burn			April burn	May 13 burn
RM Repeat May	April burn	May 1 burn	May 9 burn	May 16 burn	April burn	May 13 burn
MO Mowed	April burn	July mow*	April burn	July mow*	April burn	May 13 burn
RD Repeat Dormant	April burn	Fall burn*	Fall burn*		April burn	May 13 burn
AD Alternate Dormant	April burn		April burn		April burn	May 13 burn
NB No Burn	April burn				April burn	

* Sampling preceded treatment in year indicated.

RESULTS AND DISCUSSION

Sweet Clover Control

May Burns. Mortality of second year plants was high in all three of the stands burned in May 1978 (EM, MM, RM); frequencies in those stands were 5, 10 and 26% compared to 93-100% in the four unburned stands (Table 2). There was no difference between the stands burned May 1 (EM, RM) and May 15 (MM). The success of May burns in killing second year sweet clover was demonstrated again when Stands MO, RD and AD (which had had less successful treatments in the previous years) were burned in May, 1982, resulting in frequencies of 3, 8 and 10% for second year plants.

There was no apparent advantage to consecutive May burns, in fact Stand RM had slightly higher frequencies of first year plants. This may have been due to having more bare ground for seedling establishment as noted by Curtis and Partch (1948), and to the greater number of second year plants surviving and producing seeds after the 1978 burn.

Mowing. Mowing took place in July (1978, 1980) when the sweet clover was starting to flower. At this time most second year sweet clover plants lack axils capable of sprouting below the 15 cm cut made by the mower. Some plants however escaped the cut or were cut too high when the tractor wheels knocked them down ahead of the mower.

Since the mowed plot was burned in April the year following each of the cuts, the frequency of first year plants the year after the cut (Table 2 data for MO 1979, 1981) gives an indication of the effectiveness of the cut in preventing seeding. Each time the frequency of first year plants was lower than in Stand AD which received identical burns but was not mowed (60% in mowed vs. 95% and 100% in unmowed). Visually the differences were much more striking than the Table 2 data suggest. Frequencies in the 0.02 m² quadrats were 7% in the mowed vs. 80% and 85% in the unmowed.

Dormant Season Burns. Whether in late fall or early spring, dormant season burns stimulated germination of sweet clover. In Stands RD, AD and NB, which had only dormant season burns or no burn each year prior to the May burn in 1982, the mean frequency of first year plants the summer following a dormant season burn was 95.7% (n = 6). In the 0.02 m² quadrats the mean was 74.3%. With one exception (Stand AD, 1979) these first year plants matured well the following year. In contrast, almost none of the first year plants which germinated without a dormant season burn matured (Stand NB, 1979, 1980; AD, 1980). This was also true in the May burn stands, although the frequencies were much lower. Plants germinating after a May burn did no better than those germinating in a no burn year. Length of the first growing season may be an important factor in sweet clover survival.

Dormant season burns two years apart (AD) and four years apart (NB) had similar high frequencies of first year plants (95%, 100%) after the last dormant season burn in 1981. In the 0.02 m² quadrats the frequencies were nearly as high (85%, 90%).

After two consecutive dormant season burns (RD) there were high frequencies of both first and second year plants (1980, 1981), a situation which may make control more difficult.

TABLE 2. Frequency (%) of *Melilotus alba* in 0.5 m² quadrats (1 = first year plants; 2 = second year plants).

	1978		1979		1980		1981		1982	
	1	2	1	2	1	2	1	2	1	2
EM	0	5	5	0	0	0	5	0	0	0
MM	0	10	5	0	10	0	30	0	5	0
RM	0	26	0	0	30	0	52	0	4	4
MO	0	93	60	0	7	33	60	10	10	3
RD	0	96	96	0	96	71	87	46	25	8
AD	0	100	100	0	60	15	95	5	25	10
NB	0	100	60	0	90	0	100	0	0	75

Effects on Prairie Species

Approximately 80 species of prairie forbs and grasses were found in the quadrats in the eleven stands over the five year sampling period. The number of species per stand varied from 31 to 53 with a mean of 43. Twenty-three species occurred in 9 or more of the stands.

Each year there were many small increases and decreases in frequencies of the prairie species, but, regardless of treatment, the mean annual percentage of the species present that decreased was less than the mean annual percentage that increased or that did not change (Table 3). The stands that had either 2 or 3 consecutive no burn years (Stands NB, NB-N, EM, MM) had the highest percentage of species decreasing, while the stands that had repeated dormant burns (RD, RD-N) had the highest percentage of species increasing. There was no trend related to the success of sweet clover control. Table 3 is arranged in order of decreasing control. In the case of the paired stands there was little difference between the stand in the infested area and its non-infested ("N") counterpart. These observations suggest that the prairie species responded to the treatments more than to presence or absence of sweet clover, at least over the time period represented.

Each of the five prairie grass species that were present increased or stayed the same during the course of the experiment regardless of treatment. The dominant grasses in all the stands were *Andropogon gerardi* and *Sorghastrum nutans*, alone or in combination.

Decreasing Forb Species. Three categories of decreasers were considered: (1) forb species experiencing loss of frequency (any magnitude) during 3 or 4 of the four intervals covered by the five samples, (2) species experiencing loss of frequency greater than 10 percentage points for the period 1978-82, and (3) species experiencing loss of frequency greater than 10 percentage points in any one year. Twenty-four species fit one or more of these categories (Table 4).

As might be expected, the number of decreasing species was low in alternate year April burn stands AD and AD-N, whose treatment schedule was most similar to previous practice. The number of decreasing species was also low in repeated dormant burn stands RD and RD-N. Treatments successful in controlling *Melilotus* (EM, MM, RM, MO and MO-N) dominate Table 4, accounting for nearly three-fourths of the entries. In category 3, 1981 was the year having the greatest number of decreasers, with the mowed (Mo, MO-N), repeated May burn (RM), and one no-burn stand (NB) having 7, 4, 4 and 3 species (respectively). All plots were burned in April that year, but the observed decreases are more likely to be related to past treatments. Lag times for response to treatment are unknown, and are likely to vary among species. In the three years prior to 1981, MO and MO-N were mowed twice, RM had 3 May burns, and NB had 3 years with no burn - all treatments that represent major deviations from usual practice.

TABLE 3. Mean annual % of prairie grasses and forbs increasing, decreasing or not changing 1978-82.

Stand	Mean annual % of species		
	Increasing	Not changing	Decreasing
EM	32.9	44.5	22.1
MM	27.2	48.4	24.5
RM	37.8	42.2	20.0
MO	39.6	39.6	20.8
MO-N*	41.5	36.8	21.7
RD	49.5	32.5	17.9
RD-N*	48.4	31.5	20.2
AD	39.0	45.7	15.2
AD-N*	41.9	40.8	17.4
NB	33.4	41.1	25.6
NB-N*	37.9	37.1	25.0

* Additional stands located outside area of dense Melilotus.

TABLE 4. Species decreasing.

Species	Stand(s) in which the species decreased, by decreaser categories 1-3 (see text).		
	1	2	3
Achillea millefolium			MO-N
Anemone cylindrica			NB
Aster novaeangliae			NB,MO-N
Baptisia leucantha	EM		
Cirsium discolor			RD, RM, NB
Coreopsis palmata		NB	
Desmodium illinoense			RM
Erigeron strigosus			RM, MO
Eryngium yuccifolium			MO
Helianthus grosseserratus			MO(2X), RD
Lactuca sp.			NB
Lespedeza capitata			MO, EM, RM
Liparis liliifolia			MO, MO-N
Monarda fistulosa		RM	EM, RM
Phlox pilosa		MO	MO
Ratibida pinnata		MM, MO-N	MM, MO-N(2X),NB-N
Rudbeckia hirta	NB		RD-N
Silphium integrifolium			MM
S. laciniatum	AD-N		
S.terebinthinaceum	AD	AD	
Solidago altissima	MO	MO	MO, MO-N
S. gigantea			MO, MO-N, RD-N
S. nemoralis	EM	EM,MM,NB	EM(2X),RM,MO,NB
S. rigida		EM, RM	EM(2X)

Many of the species in Table 4 are robust, common species (e.g., *Solidago altissima, Monarda fistulosa*), or short lived, somewhat weedy species (*Erigeron strigosus, Cirsium discolor*), or species that are not typical of mesic prairies (*Liparis liliifolia*, a woodland species which was found in every stand; *Aster novaeangliae*, a wet prairie species) (Curtis 1959). The decrease of such species is not cause for great concern, and in fact some prairie managers might be looking for treatments to reduce *S. altissima* and other aggressive species.

Less common decreasers in Table 4 which historically have had limited spread in Curtis Prairie (Sperry 1983, Blewett 1981) include *Phlox pilosa* (MO), *Silphium laciniatum* (AD-N) and *Desmodium illinoense* (RM).

Several uncommon species occurred in only one quadrat in one or more stands and had disappeared by the end of the experiment. The greatest number of these (6 species, including *Phlox pilosa*) were in the no burn stands (NB and NB-N). *Phlox pilosa* also disappeared from its one quadrat in Stand MM, while *Galium boreale* and *Petalostemum candidum* did the same in Stand MO. A later study will address the problem of species that fail to establish and spread in prairie restorations.

Mowing caused some persistent changes in cover or amount of flowering which are not reflected in the frequency data, but which made the visual aspect of the mowed plot different from adjacent plots - even after four years of identical treatment. Some of the species which appeared to be affected are:

Solidago altissima, which was greatly reduced in cover and density in the mowed plots.

Lespedeza capitata, which had almost no flowers in the mowed plot for 3 years after the last cut.
Helianthus grosseserratus - big toothed sunflower, which increased substantially in cover in a well drained area where it grew with common goldenrod but decreased substantially in a wetter area where the main competitors were grasses.

Increasers. While no forb species decreased every year in any stand, 5 species increased every year: *Comandra umbellata, Lobelia spicata, Liparis liliifolia* and *Rudbeckia hirta* in RD, *Lobelia spicata* in MO, *Silphium integrifolium* in AD, and *Solidago nemoralis* in NB-N. An additional 25 species increased in 3 of the 4 intervals; 10 of these were in the repeated dormant burn stands (RD and RD-N).

The number of forb species that increased more than 10 percentage points from 1978-82 varied from 3 in Stand MM to 21 in Stand RD, and totalled 38. The best predictor of the number of species increasing in a stand was the number of dormant season burns 1977-82:

# Dormant burns	Stands	Mean # species increasing > 10 percentage points
2	EM, MM, RM NB, NB-N	7.0
3	AD, AD-N MO, MO-N	12.0
4	RD, RD-N	16.5

May burns and mowing had less influence.

Most of the 24 decreasing species (Table 4) were increasers in at least one stand having a different treatment. Thirteen of the 24 increased under repeated dormant burns (RD, RD-N).

CONCLUSIONS

The combination of an April burn followed the next year by a May burn was more successful in reducing *Melilotus alba* than any other treatment tested. Heavily infested stands having this sequence twice separated by two years without burning became almost completely free of sweet clover. Substituting consecutive May burns for the 2 intervening years without burns conferred no advantage. The similar success of early May and mid-May burns suggests that the phenological slot between the time second year sweet clover has developed enough to be vulnerable and the time prairie growth makes burning more difficult is long enough to allow burn rescheduling should weather be uncooperative or burn crews unavailable. Mowing in July, while less effective in killing second year sweet clover plants than burning in May, reduced sweet clover substantially and may be useful in situations where burning is difficult or as a follow-up to kill second year sweet clover plants surviving a May burn. Selective hand cutting might be used for small areas.

Although treatments successful in controlling sweet clover were associated with more decreases in prairie forb frequencies, the changes were small and many of the species involved are widespread and easily established. Repetition of the treatments over a longer period of time might be more serious The observed small decreases in frequency and vigor of some prairie forbs in the mowed plots, for example, might reach threatening levels in plots mowed in summer on a regular basis over a long period of time.

Schedules that included only combinations of dormant season burns and no-burn years maintained high sweet clover frequencies. Dormant season burns (either late fall or early spring) not only stimulated germination of sweet clover but also increased the chance that the seedlings would survive to become second year plants and produce seeds. Where sweet clover is present, a dormant season burn should be followed the next year by a May burn or by mowing or clipping in July. However, the direct relationship of increases in prairie forb frequencies to the number of dormant season burns (regardless of additional treatment) suggests that dormant season burns should continue to be an important part of long-term prairie management, supplemented as needed with short-term alternate treatments for troublesome species.

The apparent lack of response of prairie forbs to the presence or absence of sweet clover may have been due simply to the short time involved. It might also reflect the persistence of prairie plants under temporary adverse conditions, since the frequency data do not distinguish between suppressed and vigorous individuals. Because sweet clover is a biennial and is dependent on chance weather conditions (perhaps including a long growing season) for completion of its life cycle, its impact on the prairie may vary considerably from year to year. A dense cohort of 2nd-year plants in a year having favorable early summer growing conditions (as in 1978) may overtop the prairie plants, greatly suppressing growth and flowering, but such occurrences are likely to be sporadic; in other years the prairie species can grow and flower, conceivably even benefiting from the nitrogen input of the sweet clover.

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THE IMPACT OF PRESCRIBED BURNING ON GROUND-NESTING BIRDS

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Abstract. A study to determine the response of certain ground-nesting birds to burning and grazing is being conducted on native prairie at the Lostwood National Wildlife Refuge in northwestern North Dakota. Prescribed burns were conducted on the same 115 ha in mid-June of 1982 and 1984. Approximately half of the nests were terminated before the burns were conducted. At the time of the burns, 69% of the active clutches survived the fire; 37% eventually hatched. Several nests were initiated after the burns. Burning an area during the nesting season does not always eliminate its production for that year. Depending on the time and severity of the burn, many clutches have time to hatch before and after the burn and a considerable number may survive the fire.

INTRODUCTION

In the northern Great Plains, the use of prescribed burning as a management tool has increased dramatically in the past decade. Burning is often conducted in May and June to invigorate native grasses and suppress woody species. This is the same time of the year when many birds are nesting.

Although much concern has been expressed over the fate of nests in burned areas, little published information is available on the effect of prescribed burning on ground-nesting birds during the nesting season. No information was found documenting the fate of nests before, during, and after a prescribed fire.

We are studying burning and grazing systems and their effects on native prairie vegetation and wildlife. The study is being conducted on 4 study areas in North Dakota. One objective of this study is to determine the impact of prescribed burning on ground-nesting birds. The data presented in this paper pertain to this objective and were collected on the Lostwood National Wildlife Refuge study area in northwestern North Dakota.

STUDY SITE

The 10,829 ha Lostwood National Wildlife Refuge is in northern Mountrail and southern Burke counties, approximately 26 km west of Kenmare, North Dakota. Lostwood is characterized by rolling mixed-grass prairie interspersed with numerous lakes and wetlands. The refuge is in a region known as the "Coteau du Missouri," meaning "hills of the Missouri." The coteau extends across North Dakota from northwest to southeast and constitutes one of the most important duck production areas in the country. The soils are comparatively thin and rocky with occasional exposed gravel areas. The upland portion of the refuge is mainly a cool-season, *Agropyron-Stipa*, mixed-grass prairie with western wheatgrass (*Agropyron smithii*), blue grama (*Bouteloua gracilis*), needle-and-thread grass (*Stipa comata*), and green needlegrass (*Stipa viridula*) as the dominant grasses (Kuchler 1964). The prairie also contains considerable amounts of western snowberry (*Symphoricarpos occidentalis*) and silverberry (*Elaeagnus commutata*), with quaking aspen (*Populus tremuloides*) around some of the wetlands, and would be considered in poor range condition.

The climate in this area is cool and semi-arid, characterized by cold dry winters and warm summers. Temperatures range from an average of -15° C in January to an average of 21° C in July. Average annual precipitation is 31.8 cm, with over 50% occurring

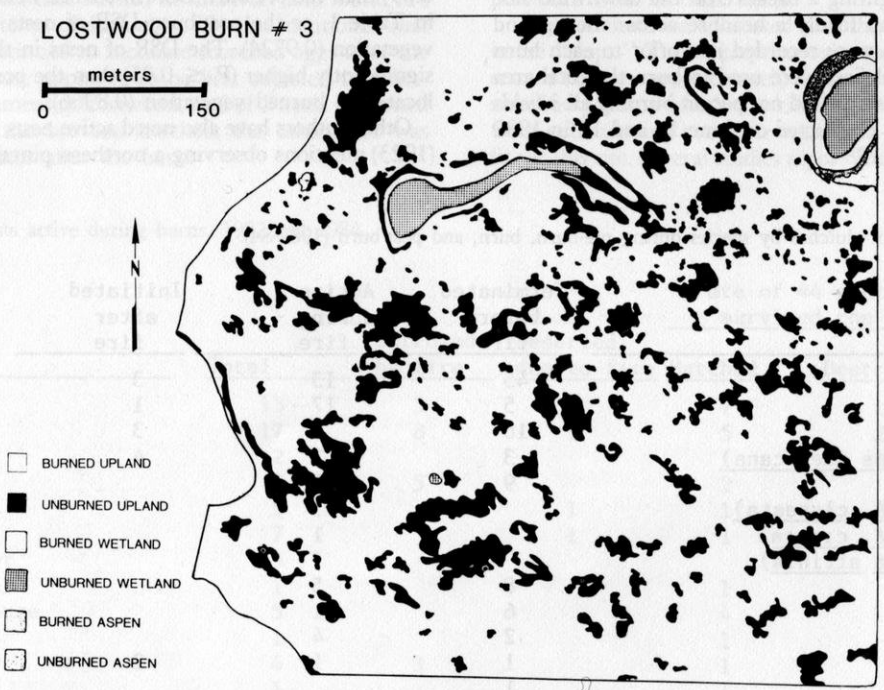

FIG. 1. Forty ha partial burn showing "mosaic" of burned and unburned upland vegetation.

TABLE 1. Environmental conditions during prescription burns on Lostwood National Wildlife Refuge, North Dakota.

Date	Time	Wind speed direction-behavior	Dry bulb	Wet bulb	Percent relative humidity
Burn 1 - 6/14/82	1430-1930	5-10 km/h SW - steady	22°C	16°C	34
Burn 2 - 6/15/82	1430-2000	0-16 km/h N - variable	24°C	17°C	39
Burn 3 - 6/19/84	1100-1600	8-16 km/h SE - steady	22°C	17°C	65
Burn 4 - 6/25/84	1140-1600	3-13 km/h NW - variable	27°C	19°C	50

from April through July. Average length of the frost-free season is 160 days (Jensen 1971).

The 6 study fields were randomly selected from 14 fields in which pre-treatment data had been collected in 1980 and 1981. Selection was based on homogeneity of vegetation, range sites and numbers of ground nesting birds. The 3 fields selected for burning ranged in size from 35 ha to 42 ha and totaled 115 ha. The 3 control fields totaled 107 ha and ranged in size from 29 ha to 42 ha.

METHODS

A 53 m long cable-chain drag (Higgins et al. 1977) was used to find nests from mid-April through mid-July of 1982 and 1984. Four nest searches were conducted annually on each field. Nest searching was usually conducted between 0700 and 1400 hours. Fields were searched prior to burning and nests were marked with fireproof markers. Descriptive data on the nest and surrounding vegetation were collected at all upland nests of waterfowl, game birds, raptors, and shorebirds. All nests were revisited immediately before and after each burn to determine the effects of the fire on nests and nesting sites. We considered a nest successful if at least 1 egg hatched. Nest success and daily survival rate (DSR) were calculated according to the methods described by Johnson (1979). Nests that were deserted or destroyed because of our disturbance, or could not be relocated, were omitted in calculations of nest success.

All 3 fields were burned using the "surround" fire method. This method involves lighting a backfire on the downwind side followed by flankfires and finally a headfire across the upwind side. Weather conditions were recorded just prior to each burn (Table 1). Two individual fires were used to burn the total area in both 1982 and 1984, as time did not permit burning all 3 fields in one day. Burning was conducted on June 14 and 15 in 1982 and June 19 and 25 in 1984.

RESULTS AND DISCUSSION

During the 2 years, 146 waterfowl, 13 sharp-tailed grouse (*Tympanuchus phasianellus*), 7 short-eared owl (*Asio flammeus*), 6 northern harrier (*Circus cyaneus*), 4 mourning dove (*Zenaida macroura*), and 1 killdeer (*Charadrius vociferus*) nests were found on the 115 ha burned. Of these 177 nests, 96 were terminated before the fire was set, 68 were active at the time of the burn, and 13 were initiated after the fire. Tables 2, 3, and 4 give the breakdown and fate of these nests. During the 2 years, 14.5% of the upland vegetation did not burn and 31% of the nests active at the time of the fire were in these unburned "skips." Thirty-one percent of all active nests were destroyed by the fire. Sixty-eight percent of the nests located in the burned vegetation (nests with vegetation burned on at least 1 side of the bowl) were destroyed by the fire. Twenty-two nests in the burned vegetation survived the fire. Eight of these hatched, 10 were destroyed by predators after the burn, and 4 were deserted after the burn. Sixteen of the 22 nests were of waterfowl and these had a DSR of 0.8966 for the period following the burn. This was significantly different ($P \leq 0.05$) than the pre-burn DSR of 0.9566.

During these same years the control fields had 151 waterfowl, 12 sharp-tailed grouse, 7 northern harrier, 2 short-eared owl, 2 mourning dove, 1 upland sandpiper (*Bartramia longicauda*), 1 Wilson's phalarope (*Phalaropus tricolor*), and 1 willet (*Catoptrophorus semipalmatus*) nests. The DSR of waterfowl nests in the control fields (0.9576) was not significantly different ($P \leq 0.05$) than the pre-burn DSR in burned fields (0.9566), as shown in Table 1, or the post-burn DSR of nests located in unburned vegetation (0.9724). The DSR of nests in the control fields was significantly higher ($P \leq 0.05$) than the post-burn DSR of nests located in burned vegetation (0.8966).

Other authors have also noted active nests following a fire. Bent (1923) mentions observing a northern pintail (*Anas acuta*) from

TABLE 2. Total number of clutches by species during pre-burn, burn, and post-burn (1982-84).

Species	Terminated before fire	Active during fire	Initiated after fire	Total
Mallard	45	13	3	61
Gadwall	5	17	1	23
Northern pintail	16	2	3	21
American wigeon (Anas americana)	3	7	4	14
Blue-winged teal	9	5		14
Northern shoveler (A. clypeata)		5		5
Green-winged teal (A. crecca)		1		1
Lesser scaup (Aythya affinis)		7		7
Sharp-tailed grouse	8	5		13
Short-eared owl	6	1		7
Northern harrier	2	4		6
Mourning dove	1	1	2	4
Killdeer	1			1
Total	96	68	13	177

TABLE 3. Daily survival rates of waterfowl nests before, during, and after the burns. Calculated by the 40% Mayfield method.

	Number of nests*	Daily survival rate	Mayfield success**
Pre-burn	120	0.9566[a, b]	22%
Day of burn			
Burned vegetation	30	0.3667[c]	0%
Unburned vegetation	12	0.9167[c]	5%
Total	32	0.5238	0%
Post-burn			
Burned vegetation	16	0.8966[a, d]	2%
Unburned vegetation	22	0.9724[b, d]	39%
Total	41	0.9551	21%

* Some nests active in more than 1 survival period.
** Average days to hatching = 34.
a, c, d Daily survival rates significantly different ($P \leq 0.05$).
b Daily survival rates not significantly different ($P > 0.05$).

a distance of 0.8 km that was incubating a clutch of scorched eggs on a tract of burned prairie. Bird (1930) describes a northern pintail hen that continued to incubate eggs scorched on May 2 until the first week in August. Leady (1950) gives an account of a search for nests on 0.8 ha of burned prairie and brush in Ohio. He flushed a mallard (*A. platyrhynchos*) and an American black duck (*A. rubripes*) from nests in an area that had been completely burned and had no cover remaining around the nest. The mallard nest contained 5 scorched and 4 unscorched eggs, the latter apparently having been laid after the fire. The American black duck nest contained 12 eggs, all blackened on 1 side by the fire. This nest had been relined with down and the female had been incubating the eggs for a week after the fire. When these nests were revisited 2 days later, they were still being tended by the hens. On the final visit, 20 days after the fire, both clutches had been destroyed. Moyle (1964) searched 336 ha of prairie and wetland nesting habitat that burned in mid-May and found fire had destroyed 30 clutches of duck eggs. He also mentioned that some of the hens continued to incubate scorched eggs after the fire. Sharp-tailed grouse appeared to be best adjusted to a fire-changed nest environment at Lostwood, as 4 of 5 nests in burned vegetation survived the fire and hatched; the other nest was destroyed by a predator after the burn.

FIG. 2. Green-winged teal nest which survived a hot burn in Canada thistle (*Cirsium arvense*), western snowberry, and quaking aspen. This nest later hatched.

Unburned vegetation "skips" within burned areas occurred in both 1982 and 1984 and most of these skips were in dense patches of western snowberry which had little or no understory vegetation. The shortage of fine fuels and environmental conditions (relatively slow wind speeds in 1982 and fairly high relative humidities in 1984) probably contributed to these partial burns. Kruse et al. (1983) stated that conditions associated with partial burns are relative humidities $> 50\%$, temperatures $< 21°$ C, and wind speeds < 10 km/h. They also mentioned that these conditions occur most often during May and June. The "skips" or unburned vegetation in the burns contained 20 clutches of eggs at the time of the burn. Fifteen of these hatched, 4 were destroyed by predators, and 1 was deserted. No significant difference ($P > 0.05$) was noted between the 0.9566 pre-burn DSR and the 0.9724 post-burn DSR of these nests.

Thirteen nests were initiated after the burns; all but 1 occurred in the "skips." The 1 exception was a gadwall (*A. strepera*) which started her nest approximately 4 days after the burn in a western snowberry clump which was killed by the fire, but the dead stems were still standing complete with dead leaves, indicating a cool fire at this site. Several studies report finding ground-nesting birds

TABLE 4. Fate of nests active during burns, 1982 and 1984.

				Fate of 44 nests that survived the fires		
Species	Total	Destroyed by fire	Deserted due to fire	Hatched	Destroyed	Deserted
Mallard	13	5		7	1	
Gadwall	17	8	1	5	2	1
Northern pintail	2			1	1	
American wigeon	7	5		2		
Blue-winged teal	5		1	1	2	1
Lesser scaup	7		1	1	3	2
Northern shoveler	5				5	
Green-winged teal	1			1		
Sharp-tailed grouse	5			4	1	
Short-eared owl	1			1		
Northern harrier	4	3		1		
Mourning dove	1			1		
TOTAL	68	21	3	25	15	4

FIG. 3. Field crew rechecking nests immediately after a burn; note mosaic of burned and unburned vegetation in background.

on areas recently burned. Glover (1956) found 3 blue-winged teal (*A. discors*) nests 5 weeks after a 28 ha April burn in Iowa. None of these clutches hatched. He also searched 2 other areas burned in April and early May of 1949 and found no duck nests during that nesting season. He concluded that the detrimental effects of burning were reflected in teal nesting populations as much as a year after the fire. Keith (1961) found 17 of 29 northern pintail nests on ground completely denuded of vegetative cover by an April 13 prairie fire. He noted that some of these hens nested only a couple of meters from unburned areas with excellent cover and that no other species nested on the burn. Forty-six percent of these northern pintail clutches were successful. Fritzell (1975) found few nests per acre but higher rates of nesting success on burned as compared to unburned areas in Manitoba. He concluded that controlled burning is an efficient tool in wildlife habitat management, but that indiscriminant annual burning reduces the quantity and quality of waterfowl nesting cover. Fritzell (1975) had one of the only studies that looked at waterfowl nesting and burning during the nesting season, but his study did not indicate how many nests survived a fire.

In other studies, Page and Cassel (1971) found no waterfowl nests on a recently burned railroad right-of-way in North Dakota and Erwin and Stasiak (1979) found complete destruction of 38 ring-necked pheasant (*Phasianus colchicus*), 2 northern bobwhite (*Colinus virginianus*), and 1 mallard nest by a fire on a 22.8 ha burn of seeded native grass in Nebraska.

In summary, burning an area during the nesting season does not necessarily eliminate the total production of ground-nesting birds for that year. Land managers who burn during the nesting season and are concerned about nesting birds should consider partial burns as a management tool. Partial burns will probably have less impact on total vegetation changes but should result in higher recruitment of birds than would complete burns.

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THE EFFECT OF FALL BURNING ON SMALL MAMMALS IN BLUE MOUNDS STATE PARK, LUVERNE, MINNESOTA

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Abstract. The effect of a fall prescribed burn on the populations of six species of small mammals was investigated by live trapping at Blue Mounds State Park, Luverne, Minnesota. The animal species studied include the prairie deer mouse (*Peromyscus maniculatus*), the meadow vole (*Microtus pennsylvanicus*), the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*), the western harvest mouse (*Reithrodontomys megalotis*), the grasshopper mouse (*Onychomys leucogaster*), and the short-tail shrew (*Blarina brevicauda*). The long-tail weasel (*Mustela frenata*) was captured twice during the study. No preference was found for either the burned or unburned area for any species 10 months after the burn. The small mammal populations were not severely affected by burning; thus the practice of prescribed burns as a prairie management tool should continue in the fall of the year.

DESCRIPTION OF THE STUDY AREA

Blue Mounds State Park, located in Rock County, which is bordered by Iowa to the south and South Dakota to the west, is one of Minnesota's largest native prairie state parks at 660 hectares.

A large Sioux Quartzite outcropping is the main geographical feature of the park. Due to bedrock outcroppings, soil depths are relatively shallow, but do vary from bare rock to 1.8 meters deep, leading to good examples of tall grass, mid grass and short grass environments.

Generally, soil types in southwestern Minnesota are classified as mollisols (Brady 1974). Within the park, soils are classified as Ihlen Rock Outcrop Complex with pH being neutral to slightly acid in the low to high 6 range (Magozzi 1980).

Prior to 1974, much of the park was in private ownership and grazed by livestock (Magozzi 1980). The study areas were located near the Blue Mounds Interpretive Center within a part formerly utilized for grazing. After grazing was eliminated, the native plant species made a dramatic comeback.

One third of each study area, characterized by very shallow well-drained soil, was a short grass prairie community. Dominant grasses included Blue Grama (*Bouteloua gracilis*), Canada Bluegrass (*Poa compressa*), Prairie Dropseed (*Sporobolus heterolepis*), and Stonyhills Muhly (*Muhlenburgia cuspidata*). The most visual broadleaf herbaceous plants included Canada Goldenrod (*Solidago canadensis*), Heath Aster (*Aster ericoides*) and two species of cactus, the Western Prickly Pear (*Opuntia humifosa*) and the Brittle Prickly Pear (*Opuntia fragilis*).

Two thirds of each study area had deeper, water-absorbing soil leading to a tall grass prairie community. Dominant grasses included Big Bluestem (*Andropogon gerardi*), Indian Grass (*Sorghastrum nutans*), Little Bluestem (*Andropogon scoparius*) and Side Oats Grama (*Bouteloua curtipendula*). The most visual broadleaf plants included Canada Goldenrod (*Solidago canadensis*), Stiff Sunflower (*Helianthus rigidus*), Tall Sage (*Salvia pitcheri*) and Snowberry (*Symphoricarpos albus*). During the research many individual flowering Downy Gentian (*Gentiana puberula*) were observed.

The burn left almost no litter. During the following growing season, because of excessive plant growth, possibly stimulated by the fire, the vegetation was very thick and a small amount of litter, 2.5 centimeters or less, had accumulated.

Litter had accumulated in the unburned study area since 1974 when grazing by livestock ceased. The litter depth varied from 2.5 to 25 centimeters and averaged 17.5 centimeters. The litter build-up noticeably affected the growth and maturation of vegetation when compared with the burned area. Similar results have been described in other fire-related small mammal studies (Springer and Schramm 1972, Beck and Vogel 1972).

METHODS

Species diversity of small mammals in the research area was determined by live trapping. The research area consisted of two 0.72 hectare plots. Plot A was located within an area burned in November 1980, and Plot B was located outside of the burn area approximately 90 meters from the fire line. Each trap area was set in a 12 meter grid pattern of 7 rows and 7 traps per row. Traps used were similar to those described Frydendall (1969) and were baited with a combination of peanut butter and sunflower seeds.

Trapping began 10 months after the burn and was in operation from September 1 through September 30, 1981, with the exception of September 5th and 6th. Traps were checked daily between 8:00 a.m. and 10:00 a.m. Captured individuals, with the exception of the long-tail weasel (*Mustela frenata*), were marked by toe clipping and released.

Nomenclature for mammals follows Hall (1981), and that for plants follows Fernald (1970).

CLIMATOLOGICAL DATA

The 1980-81 winter following the November burn was unusually mild. Comparisons of temperature and snowfall average for the winter of 1980-81 (November - March) to overall winter averages are as follows: snowfall for 1980-81 was 22.5 centimeters and the overall average is 90 centimeters; average temperature for 1980-81 was -1.46 degree centigrade and the overall average is -5.21 degrees centigrade (Mitchell 1980, 1981).

All precipitation during the 1980-81 winter was in the form of snow. The only length of time snow remained on the ground was in February. The 16 days of snow cover in February were not continuous and break down as follows: 4 days had a 12.5 cm snow cover, 10 days had a 7.5 cm snow cover, and 2 days had a 2.5 cm snow cover (Mitchell 1980, 1981).

RESULTS

Five species of small rodents, the prairie deer mouse (*Peromyscus maniculatus*), the meadow vole (*Microtus pennsylvanicus*), the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*), the western harvest mouse (*Reithrodontomys megalotis*), the grasshopper mouse (*Onychomys leucogaster*), and one species of insectivore, the short-tail shrew (*Blarina brevicauda*) and one species of the family mustelidae, the long-tail weasel (*Mustela frenata*), were recorded during the study. With the exception of the grasshopper mouse and the long-tail weasel, the species recorded in this study correlate with those reported in this area of the state by Ernst and French (1977). According to Ernst and French (1977) the grasshopper mouse is rare, of local occurrence, and has not been recorded from Rock County. The long-tail weasel is uncommon and has been recorded from only two southwest Minnesota counties, Rock County not included (Ernst and French 1977).

TABLE 1. Species and total number of captures on plots A and B at Blue Mounds State Park.

	Individuals			Captures		
	A	B	Total	A	B	Total
Deer mouse	9	7	15	12	18	30
Meadow vole	10	7	17	15	9	24
13-lined ground squirrel	10	13	19	91	53	144
Harvest mouse	6	4	10	7	5	12
Grasshopper mouse	2	1	2	4	5	9
Short-tail shrew	4	1	5	4	1	5
Long-tail weasel	1	1	2	1	1	2
TOTAL	42	34	70	134	92	226

Totally, 226 captures of 70 individuals in 2,744 trap nights were recorded, representing an 8.2% capture success (Table 1).

In the burned area, Plot A, there were 134 captures of 42 individuals in 1,372 trap nights, representing a 9.7% capture success. Whereas, in the nonburned area, Plot B with 92 captures of 34 individuals in 1,372 trap nights, represented a 6.7% capture success (Table 1).

Discrepancy between the overall number of individuals captured and the total number of individuals for each plot was due to a cross over between plots, which included four thirteen-lined squirrel, one deer mouse and one grasshopper mouse.

Though capture success differs slightly between plots, when statistical analysis using Chi-square was applied to the total number of individuals for each plot, no preference was found for either area 10 months after the burn took place. The results were the same when analysis was applied to individual species.

DISCUSSION

These results correspond with other fire-related small mammal studies. However, the burn in this study was in the fall, and similar studies, with the exception of Cook (1959), researched the effects of a spring burn.

Lyon (1978), in a review of 360 papers, and Erwin and Stasiak (1979) found vertebrates are rarely killed in fires. In contradiction, Ver Steeg (1983) reported 57 dead meadow voles following an early spring burn. No dead small mammals were found in a post fire inspection of the burn area in this study.

Few small mammals were trapped up to a month following a fire (Cook 1959, Moreth and Schramm 1973, Fala 1975, Schramm and Willcutts 1983). This has been attributed to the abrupt habitat change brought about by fire.

During the growing season following a burn, many investigators including Moreth and Schramm (1973), Fala (1975), and Schramm and Willcutts (1983), found the prairie deer mouse to be one of the first small mammals to reestablish in a burn area. This early return was apparently because of ease of locomotion due to lack of vegetation litter (Schramm and Willcutts 1983). No preference between the burned and unburned areas was found in this study.

The meadow vole constructs runways beneath the litter for efficient movement. Thus, a grassland with dense accumulations of litter would be the preferred habitat of the meadow vole (Schramm and Willcutts 1983). Schramm (1970), Moreth and Schramm (1973), Fala (1975), Hessenius (1980) and Schramm and Willcutts (1983) all reported a sharp reduction in meadow vole populations following a fire. Cook (1959) found the same for the California vole (*Microtus californicus*). These vole populations in the above mentioned studies did not make a comeback until well into the vegetational growing season. Cook (1959) and Fala (1975) found populations back to near normal numbers after two growing seasons. No preference between the burned and unburned areas was found in this study, indicating that near the end of the first growing season both study plots had similar habitat conditions.

Beck and Vogel (1972) and Hessenius (1980) found the thirteen-lined ground squirrel preferred burned over unburned areas. Lyon (1978) suggested the increased light and temperature of a burn area, due to the darkness of charred vegetation and soil, may favor ground squirrels. Hessenius (1980) felt the preference was associated with the openness which allowed more visual observation for detecting and escaping predators. No preference was found between burned and unburned areas in this study indicating that habitat requirements for the thirteen-lined ground squirrel were being met in both study plots.

Three species, the grasshopper mouse, the western harvest mouse and the short-tail shrew, were caught infrequently on both study plots in this study and individual preference were not determined. Springer and Schramm (1972) found the short-tail shrew needed a litter build up after a fire before populations would reach maximum density. Because they were captured on both study plots, habitat requirements for the short-tail shrew must have been met near the end of the first growing season. Schramm and Willcutts (1983) found the western harvest mouse in low numbers and evenly distributed with no apparent preference for burn or control areas. Similar results were found in this study. The grasshopper mouse is rare in southwest Minnesota (Ernst and French 1977). The capture of this species in this study was the first indication of its presence in Rock County.

Besides the prairie burn other factors possibly influenced the results of this study. Frydendall (1969) found non-hibernating small mammal populations adversely affected by winter kill. The weather during the winter following the burn is this study was unusually mild (Mitchell 1980-1981). The mild weather possibly helped to overwinter a higher percentage of individuals, thus maintaining a high spring breeding population. Also, the early vigorous growth of vegetation in the spring following a fire usually improves food supplies (Lyon 1978). Combining these two factors, (1) a high carry over population due to the mild winter and (2) an improved food supply, a crowded small mammal population possibly migrated from surrounding unburned areas and utilized the revitalized burn area.

SUMMARY AND CONCLUSION

The population dynamics of six species of small mammals was investigated in relation to the effect of a fall prescribed burn. A definite effect on small mammal populations immediately following a fire had been reported by numerous investigators including Fala (1975), Schramm and Willcutts (1983), and Ver Steeg (1983). This effect has been attributed to the abrupt habitat change brought about by fire. No small mammal species indicated a preference between burned and unburned prairie in this study 10 months after the burn. The burned vegetation responded rapidly. Within a year after the burn had reestablished enough to meet the habitat requirements of the small prairie mammals. Beck and Vogel (1972) mentioned that repeated burnings, not allowing the accumulation of vegetation litter, can have long term detrimental effects on small mammals. Springer and Schramm (1972) indicated the short-tail shrew needed that vegetation litter to get maximum population densities. Cook (1959), Schramm (1970), and Schramm and Willcutts (1983) indicated the meadow vole needed vegetation litter

to meet habitat requirements. However, small fall burns, 100 acres or less, with intermittent periods of litter accumulation would appear to have no long term detrimental effect on small mammal populations at Blue Mounds State Park.

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Part 7. PRAIRIE PRESERVATION AND INTERPRETATION

BLUESTEM PRAIRIE INVENTORY IN THE RED RIVER VALLEY, NORTH DAKOTA

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Abstract. A bluestem prairie inventory was conducted in the Red River Valley of North Dakota during 1982-1983. Potential bluestem prairie remnants were identified through photointerpretation of aerial color infrared transparencies, and the 809 potential remnant sites were field-checked and evaluated. Five sites representing a total area of less than 1.2 km² (1/2 mi²) were identified as possessing healthy bluestem prairie. Twenty-one more sites contained bluestem prairie which was degraded and/or predominantly composed of other prairie types on less arable land including sand prairie, mixed grass prairie, low prairie, and alkaline meadow. This signifies a state bluestem prairie habitat loss of 10,000-fold magnitude.

INTRODUCTION

Bluestem prairie is the potential natural vegetation in the Red River Valley of North Dakota (Küchler 1975). The 17,700 km² (6,800 mi²) Red River Valley area covers the eastern tenth of the state. Six bluestem prairie sites had been reported in the Red River Valley as of 1982 (Kantrud and Kologiski 1982, Stevens 1970, Ralston personal communication, Smeins 1967, Redmann 1972, Wali et al. 1973), only one supporting high quality bluestem habitat (Heidel 1982). The two region-wide prairie vegetation studies among the preceding had not incorporated exhaustive prairie remnant search methods. These facts indicated that bluestem prairie is a high inventory priority for the North Dakota Natural Heritage Inventory.

STUDY AREA

The Red River Valley plain spans ten counties in North Dakota (Fig. 1). It extends into Minnesota, Manitoba, and the far northeastern corner of South Dakota, marking the southern lobe of glacial Lake Agassiz.

This fertile plain was formed on deep fluvial and lacustrine deposits in the glacial Lake Agassiz basin. The deposited sediments obscured almost all pre-existing topography in the till-covered basin. When glacial Lake Agassiz retreated for the final time, it left a flat, uninterrupted landscape. Moderately-drained, fine- to medium-textured aquiborolls were the prevalent soils to develop in this setting (Brady 1974, Omodt et al. 1968). Dominants included big bluestem (*Andropogon gerardi*) and little bluestem (*Schizachyrium scoparium*). Approximately 75% of the Red River Valley's presettlement vegetation was bluestem prairie, a 13,000 km² area. This corresponds with the "mid prairie" of Ralston (1968), part of the "tall grass prairie" of Weaver and Clements (1938) as cited in Whitman and Wali (1975).

Elsewhere, gallery forests developed along the youthful drainage of the Red River and its tributaries. Low prairies, wet meadows, and marsh communities also lined the tributaries and occupied wetlands. A few freshwater and alkaline lakes dotted the landscape. Less than 10% of the Red River Valley's presettlement surface area was covered by these communities.

Mixed grass prairie extended onto the droughty sand and gravel deposits of the large deltas, poorly-developed beach ridges, and small areas of moraine. In some places, sand deposits were reworked by the wind. Sand prairie vegetation became established where aeolian deposits have formed prominent sand dunes. Less than 10% of the Red River Valley's surface area was covered by mixed grass and sand prairie communities, as interpreted from the surface geology map of Clayton (1980).

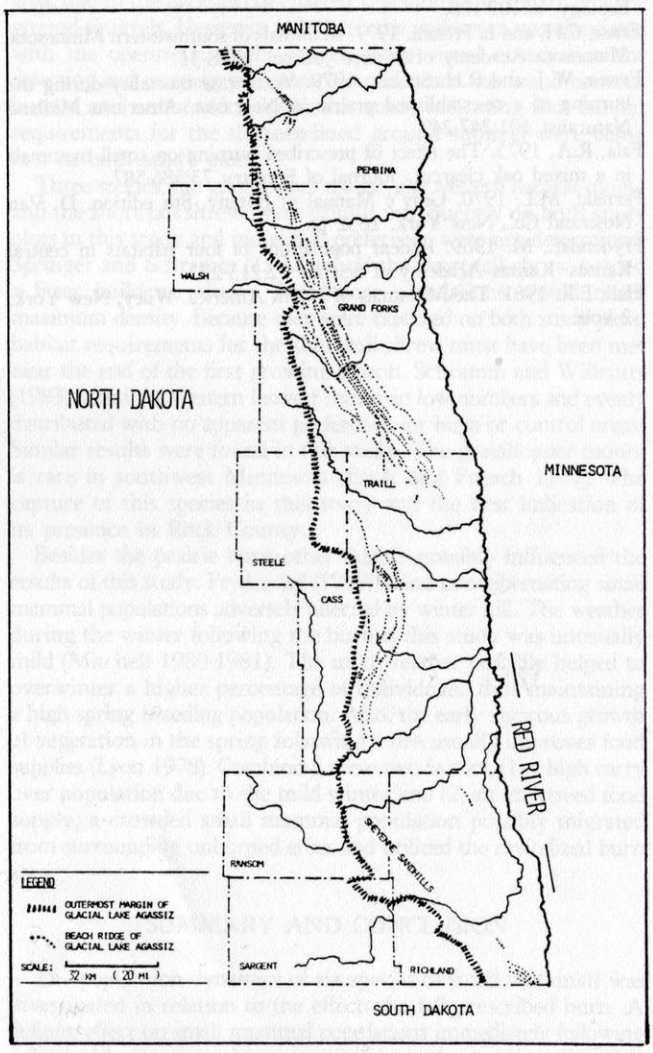

FIG. 1. Red River Valley plain of North Dakota.

Alkaline meadows developed where alkaline artesian upwellings reached the soil horizon from the Dakota Sandstone Formation (Laird 1944, Benz et al. 1961). Less than 10% of the Red River Valley's presettlement surface area was covered by alkaline meadows, as interpreted from the soils map of Omodt et al. (1968).

Postglacial development of the Red River Valley flora has been

treated for North Dakota by Rudd (1951) and for Manitoba by Love (1959). Evidence which includes subsequent pollen profile studies (Ashworth and Cvancara 1983, McAndrews 1967, Shay 1967), indicates that the Red River Valley had been predominantly prairie throughout most of the interval following final glacial Lake Agassiz retreat.

The landscape and its vegetation changed drastically with European settlement. Settlement rapidly followed initial railroad construction in 1872. By 1910 all unappropriated lands in the Red River Valley of North Dakota were sold (Murray 1967). By 1919, North Dakota ranked fifth nationwide in its net cropland acreage at 4,304,296 ha (10,760,741 acres), and also fifth in cropland proportion at 44.0% (Shantz and Zon 1924). The main thrust of this rapid prairie-to-cropland conversion was in the Red River Valley because of its nearly uninterrupted soil fertility and proximity to the earliest trade routes.

Wheat was almost the exclusive crop during the settlement period. Not until 1910 were attempts made to diversify the economy by bringing in cattle as well as other crops (Murray 1967). There were almost no incentives to set aside prairie for hayland and less consumptive uses until after most of it had already been plowed.

The paucity of information on North Dakota's Red River Valley bluestem prairie sites is, in part, due to the rapid disappearance of Red River Valley prairie prior to regional botanical research. The first flora of the state was written during settlement of the Red River Valley and included 12 principal points of plant collection in the Valley (Bolley and Waldron 1900). The second flora of the state (Bergman 1912) was printed after all the lands were appropriated, and included a section heading entitled "Disappearance of Species," with probable reference to Red River Valley prairie. The author of the third and currently used state flora, Stevens (1963), came to North Dakota in 1909. His many publications did not include documentation of Red River Valley prairie bluestem remnants on other than a small scale (Stevens 1970).

The single most complete study of Red River Valley prairie in North Dakota is that of Ralston (1968), with a companion study of aquatic vegetation by Smeins (1967). Ralston's work spanned the prairie vegetation of the entire Red River Valley, including Manitoba and Minnesota. The 33 North Dakota study sites in this research were primarily small railroad right-of-way segments with no form of protection (Ralston 1983 personal communication).

The only existing Red River Valley prairie sites in North Dakota that have binding protection also have limited bluestem prairie cover. They include Oakville Prairie and Forest River Biology Area of the University of North Dakota, and the Sheyenne National Grassland of the U.S. Forest Service.

In contrast to North Dakota, there are at least 16 Red River Valley sites in Minnesota with extensive bluestem prairie cover and having public or private nature preserve status (The Nature Conservancy 1980, Wendt 1984). Systematic prairie searches in Minnesota counties helped in identifying these prairie remnants (Pemble and VanAmburg 1973). In Manitoba, searches for and evaluations of bluestem prairie remnants have been conducted in conjunction with the International Biological Program of the International Union for Conservation of Nature and Natural Resources (IUCN). To date, there are two bluestem prairie nature preserves in the glacial Lake Agassiz basin of Manitoba. Drier prairie types are protected in the Spruce Woods Provincial Park and Spruce Woods Provincial Forest.

METHODS

Preliminary evaluations of the six reported bluestem prairie sites in the Red River Valley of North Dakota were conducted in the summer of 1982. Additional potential bluestem prairie sites were sought in the winter of 1982 through use of aerial color infrared transparencies at the scale of 1:65,000, photographed by the U.S. Fish and Wildlife Service in the National Wetlands Inventory. They were photographed in early-season flights from April to May, between 1979 to 1981. Potential bluestem prairie sites were identified from the color infrared transparencies with use of a stereoscope. Site boundaries were recorded directly onto county maps at the scale of 1:125,000. Site identification was based on presence of dual warm season/cool season floristic components as indicated by colors, on presence of ground pattern heterogeneity, and on absence of agricultural features such as furrowing and bare earth. A conservative approach was taken in the identification process with marginal areas included. For example, stockponds did not automatically warrant site exclusion.

From the known prairie sites, it was determined that prairie remnants could be identified with reasonable certainty down to 16 ha in size, with certainty dropping off sharply below 8 ha acres. A total of 809 sites were identified and mapped.

As further check, the sites identified in two of the counties, totalling 270, were evaluated against 1981 color aerial slides of the Agriculture Stabilization and Conservation Service photographed in the latter part of the 1981 growing season. The color slides provide information on land use that was, in some cases, not discernible on the color infrared transparencies. This added step generally corroborated the initial site identification, but was judged to be an inadequate substitute.

The 809 sites were ground-checked mainly between April and June 1983 in a reconnaissance to determine whether they were likely to represent native prairie remnants. Their species dominants, probable condition, and current utilization were noted.

Eighty-two sites were identified in the first screening as potentially warranting intensive evaluation. They were revisited between July 25 and August 14, 1983. Among the sites revisited were the the six previously reported prairie sites. Among the 76 new sites, two were plowed under between the time of the initial evaluation and the revisit. Excluded from consideration were the blocks of native grassland that are not bluestem prairie and which have persisted in alkaline upwellings and in the Sheyenne Sandhills.

Intensive site evaluations were actually completed for only 24 sites which were confirmed as meeting the criteria of being at least co-dominated by native grass species in the presence of Kentucky bluegrass (*Poa pratensis*). They also showed no signs of plowing, seeding, or heavy grazing. Information gathered at the 24 intensive evaluation sites included tract boundaries, identification and evaluation of natural communities present, and preparation of a preliminary vascular plant species list. The basic site information was subsequently entered into the North Dakota Natural Heritage Inventory data base.

Community composition was characterized at the best prairie sites within relatively homogeneous 30 m^2 areas through point-frame analysis. Strikes were noted on a 10-point frame placed 50 times at regular intervals along transects. Grasses were identified through use of Best et al. (1971) and Hitchcock (1971). Soil samples (100 cc) were collected from the vegetation sampling area to characterize soil textural class.

RESULTS AND DISCUSSION

A total of five sites represented healthy bluestem prairie having native species dominance and relatively high species diversity. Together they total 110 ha, less than 1.2 km in a 13,000 km area. They ranged from 7 to 44 ha. Nineteen more sites, totalling roughly 1,000 ha acres, were either degraded bluestem prairie or very localized bluestem prairie within drier, wetter, or more halophytic prairie types.

The five prime bluestem prairie sites were all arable and were mowed in the latter half of the growing season. They all had areas of saturated soils in spring. They were widely scattered from north to south, but all tended to lie toward the western edge of the Valley. One of the sites had received a deliberate measure of protection since Ralston had used it as a study site. Another

remnant had been deliberately set aside by private owners and passed down from generation to generation.

The documented net area results are not exhaustive because the methods employed were not suited to identification of sites smaller than 8 ha. This shortcoming has already been demonstrated in the form of a 4 ha prairie remnant in good condition that subsequently came to our attention. However, there is the perceived scarcity of remnants in very small sites such as railroad right-of-ways and cemeteries (Heidel personal observation). While the preceding totals are incomplete, they are interpreted as representing the great majority of remaining bluestem prairie area.

Some sites among the 785 others represent photointerpretation errors, including planted watercourses and stubble fields. Of the remainder, almost 80% were grazed and less than 10% were hayed. They had highly degraded native grassland, seeded native grassland, or non-native grassland.

Plant associations identified compare closely with previously reported associations (Ralston 1968). Clay loam soils were at both of the prairie sites having Indiangrass (*Sorghastrum nutans*) accompanying big bluestem (*Andropogon gerardi*) in dominance. Silt loams were found at both of the prairie sites having mat muhly (*Muhlenbergia richardsonis*) accompanying big bluestem and little bluestem (*Schizachyrium scoparium*) dominance. Sandy loam was at the site with prairie dropseed (*Sporobolus heterolepis*) codominant with big bluestem. One silt loam site had an unusual component of tufted hairgrass (*Deschampsia caespitosa*) as reported in Heidel (1983). This species, which had appeared to be among the dominant species by visual estimates, did not contribute greatly to basal area at the sample locale.

During the inventory, new site records for four plants considered rare in the state were also documented (*Aster sericeus, Bromus kalmii, Cypripedium candidum, Pycnanthemum virginianum*).

The results provide basis for intensive site studies and distribution information for extensive inventory of small remnants. More importantly, the results indicate a 10,000-fold bluestem prairie habitat loss in North Dakota which lends credence to statements of need for state bluestem prairie site protection.

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A COMPREHENSIVE SURVEY FOR PRAIRIE REMNANTS IN IOWA: METHODS AND PRELIMINARY RESULTS

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Abstract. The Iowa Natural Areas Inventory (INAI) has located and gathered basic ecological data on Iowa's western Loess Hills prairies, several northeast Iowa hill prairies, and large black soil prairies. Survey expansion to cover all prairie types statewide is occurring now.

Examination of infrared aerial photographs taken during cool seasons provides the most comprehensive survey for potential prairie sites. On these photos, potential prairies are gray (duff accumulation) while Eurasian grass meadows are pink (photosynthetic activity). Reports based on direct field examination were solicited from county conservation boards and county assessors' offices. The latter have records of prairies granted property tax exemptions through Iowa's "Slough Bill."

Thirty-four previously undocumented prairies have been reported by county conservation boards and fifteen by the tax assessors. Hundreds of undocumented potential prairies have been located on the infrared photographs. The most common locations found to have potential prairies are the following: (1) undrained pothole wetlands, (2) areas cut off from croplands by roads and railroads, (3) cemeteries, (4) prairie hayfields, and, especially, (5) steep slopes in stream-dissected landscapes.

Preliminary INAI work indicates that Iowa prairie remnants are more frequent than expected. However, these remnants are concentrated in a few geographic regions of the state.

INTRODUCTION

The state of Iowa lies in the heart of the tallgrass prairie region of North America (Küchler 1964). In fact, it is the only state lying totally within the Prairie Peninsula as defined by Transeau (1935). Estimates indicate that up to 85% of the state was covered by prairie in presettlement times (prior to 1840). One of the major goals of the Iowa Natural Areas Inventory (INAI), established by The Nature Conservancy as a state natural heritage program in late 1981 and now operated by the Iowa Conservation Commission, has been and continues to be the classification and documentation of remnant prairies in Iowa.

Based on literature review and consultation with ecologists statewide, a preliminary classification system for prairie communities was constructed. Geographic and topographic position, soil parent materials, and physiognomy of dominant plant species were the major factors used to create the classification. Nine prairie types are represented in the initial model. These are (see Fig. 1 for location and extent of landforms):

1. Loess Hills prairie - mixed grass prairie restricted to deep loess deposits on the Loess Hills landform bordering the Missouri River;
2. Sioux Quartzite prairie - a short to midgrass prairie on the only exposed Precambrian bedrock in Iowa, in the northwest corner of the state (only remnant of this type is protected in Gitchie Manitou State Preserve);
3. Hill prairie - a mid to tallgrass prairie on thin rocky soils over

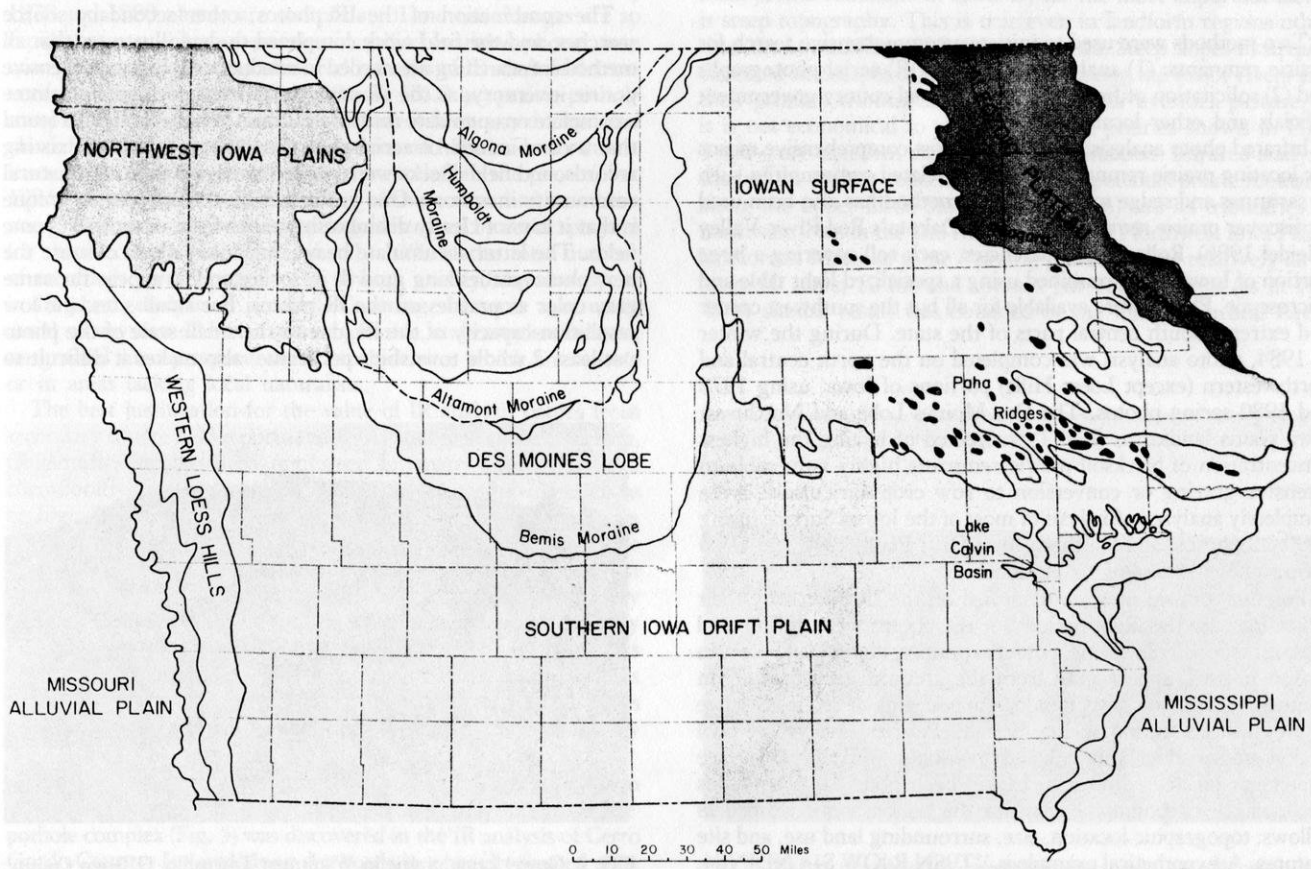

FIG. 1. Landform regions of Iowa (from Prior, 1976).

limestone bedrock on steep south to west facing exposures on northeast Iowa's Paleozoic Plateau landform;
4. Blacksoil prairie - variable tallgrass prairie (some midgrasses) on deep loam soils of level to gently rolling terrain on the Iowan Surface, Des Moines Lobe, and Northwest Iowa Drift Plain landforms;
5. Clay loam prairie - tallgrass prairie on heavily dissected Southern Iowan Drift Plain; weathered soils over impervious clay till;
6. Sand prairie - prairies on localized water-deposited sand in eastern Iowa's Lake Calvin Basin and on aeolian sands of a few eastern Iowa rivers; characterized by species restricted to sandy substrates;
7. Floodplain prairie - tallgrass prairies on alluvial soils of river and creek floodplains;
8. Gravel prairie - mid to tallgrass prairies on coarse-grained outwash deposits (sand/gravel mixture) of the Des Moines Lobe landform;
9. Limestone prairie - mid to tallgrass prairie on thin soils over sloping to level limestone bedrock, mostly on the Iowan Surface landform.

Preliminary surveys, based on known remnants, were used to rank the communities according to their rarity, biological uniqueness, vulnerability to destruction, and degree of preservation. Survey time was then prioritized to cover the highest ranking types first. While this procedure is somewhat arbitrary, and some data on remnants of all 9 types were recorded, early searches emphasized the Loess Hills prairies, virtually unique to Iowa, hill prairies, because very few are preserved, and larger level blacksoil remnants, once most typical of Iowa and continuously threatened by conversion to row crops. The survey was then expanded in 1984 to cover all prairie types, with the goal of achieving a comprehensive statewide prairie inventory.

METHODS

Two methods were used to initiate a comprehensive search for prairie remnants: (1) analysis of infrared (IR) aerial photographs and (2) solicitation of field reports from local county government officials and other local residents.

Infrared photo analysis provides the most comprehensive means for locating prairie remnants, as well as related communities such as savannas and sedge meadows. This method has also been used to discover prairie remnants in North Dakota's Red River Valley (Heidel 1986). Rolls of transparencies, each roll covering a large portion of Iowa, were examined using a specialized light table and microscope. Photos were available for all but the southwest corner and extreme south central parts of the state. During the winter of 1984, photo analysis was completed on the north central and northwestern (except Loess Hills) portions of Iowa, using 1978 and 1980 spring photos. The Des Moines Lobe and Northwest Iowa plains landforms (Fig. 1), suspected of having the highest concentration of blacksoil prairie remnants highly vulnerable to intensive grazing or conversion to row crop agriculture, were completely analyzed. Analysis of most of the Iowan Surface (using 1980 fall photos) and Southern Iowa Drift Plain (1978 and 1980 spring photos) remains to be done.

Potential prairie sites are identified on the IR photos by their color. Because the flight periods for the photos were during cool seasons, especially in spring, potential prairies, dominated by warm season grasses, appear gray from the accumulation of duff. In contrast, cool season grass meadows appear pink or red from active photosynthesis during spring (or fall). Prairies invaded by cool season grasses show both pink and gray tones, with the percentage dependent on degree of disturbance. Each potential prairie was outlined on a topographic map for the region and described as follows: topographic location, size, surrounding land use, and site features. A hypothetical example is "T98N R4OW S14 NE4NE4, 10 acres on a long narrow west-facing slope above river, cropland to east and west, pasture north and south, high quality prairie potential (solid gray tones)." All written records were filed by county for future field inspection by INAI staff or prescreening by county level naturalists.

Records of prairie remnants confirmed by field sightings were garnered from two directly solicited sources and by reports from residents interested in prairie throughout the state. These reports confirmed or added to the IR analysis records. Iowa has an extensive system of county conservation boards; 98 of the state's 99 counties have such boards and many are actively interested in the identification and protection of prairie remnants (Walker 1984, Roosa 1976). Records of prairies, specifically those owned by the boards themselves, were sought through an article in the monthly statewide county conservation board newsletter. The second directly solicited source was a prairie record form sent to all 99 county tax assessors. Through Iowa's "Slough Bill," landowners are allowed to remove native prairies from the property tax rolls each year by registering their prairie tract with the county assessor. Sites are confirmed as prairies by county officials able to identify prairie.

RESULTS AND DISCUSSION

The INAI data base now contains many more prairie records as a result of the 1984 IR analysis and secondary reports. Thirty-four previously undocumented prairies were reported through the canvass of county conservation boards; fifteen new prairies registered on the Slough Bill were reported by county tax assessors. Over 200 additional prairies are known from a variety of secondary sources, including state scientists, wildlife biologists, county conservationists, and knowledgeable local residents. The infrared analysis identified over 1,000 potential prairie sites. However, over 80% of these sites have not been field checked for quality, so as yet an estimate of the true total number of newly discovered prairies is not available.

The combination of the IR photos, other secondary source searches, and the field work completed to date illustrates that all methods of searching are needed to conduct a truly comprehensive prairie inventory, as the IR analysis by itself does not guarantee a complete or up-to-date record. In Illinois White (1981) also found that a combination of aerial photo analysis, a search of existing records, and field checks were needed to have a thorough natural community inventory. One problem with the infrared technique is that it cannot clearly distinguish prairies from unmowed brome fields. The latter accumulate heavy duff loads which obscure the new photosynthesizing growth in spring and so appear the same gray color as prairies on the IR photos. For small sites, the low resolution capacity of the IR (due to the small scale of the photo - at least 2 whole townships per frame) also makes it difficult to

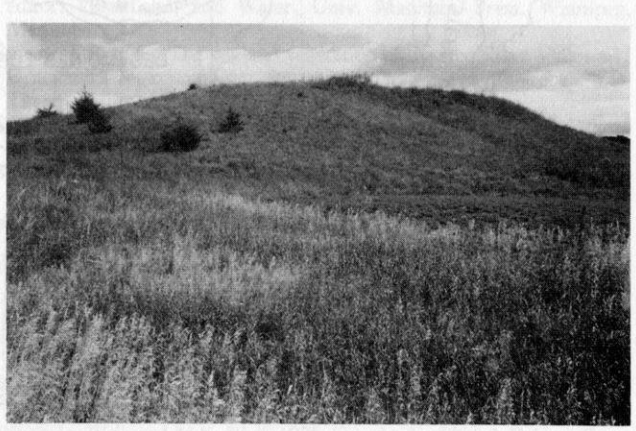

FIG. 2. Gravel kame prairie in Waterman Township, O'Brien County, Iowa.

FIG. 3. Limestone prairie, largest in Iowa, on long steep south to west facing slope, Cerro Gordo County.

FIG. 4. Portion of largest prairie-savanna complex known in Iowa, on steep, stream-dissected land of the Little Sioux River valley, Clay County.

distinguish praires from Eurasian grass meadows.

Small size and resolution problems cause prairies to be overlooked on IR photos. For example, despite an intensive IR search of Waterman Township in O'Brien County in northwest Iowa, a 5 acre (2 ha) gravel kame prairie (Fig. 2) was completely overlooked. It was discovered while looking at numerous other larger areas of lesser quality that were identified by IR analysis. Similarly, a 17 acre (6.9 ha) level blacksoil prairie in nearby Buena Vista County was overlooked on the photos (fortunately, it was known from a county board report). Areas of high quality prairie on the site were overlooked because the resolution of the IR photo did not clearly distinguish the prairie patches within large areas dominated by brome and timothy.

Far more important than these problems is the fact that even 1978 and 1980 photos are out of date. Land use changes are so rapid that a number of prairies identified in these photos may now be destroyed or degraded. Field checks of IR-identified areas verify this fact. For example, a 40 acre (16.2 ha) prairie pothole complex in Palo Alto County in northwest Iowa was drained and plowed in 1982. Several pastured prairies on hillsides in northwest Iowa appeared covered with prairie grass duff in the photos, but 1984 field checks showed that many of these areas had now been overgrazed and some were completely destroyed by aerial spraying for thistle control. However, if only 10% of the total number of recorded prairies prove to be of high quality, the time spent in IR photo analysis is justified. Covering the same area using aerial surveys would be far more expensive, and complete reliance on ground survey reports would exclude sites which are remote or in areas lacking local naturalists.

The best justification for the value of IR analysis comes from secondary source field reports and INAI staff field checks. To date, IR-identification has been reinforced for many sites by these 2 corroborative methods, and several of these sites have proven to be high diversity, high quality prairies, not simply prairie grass stands devoid of prairie indicator forbs. For example, both the steep hillside limestone prairie in Cerro Gordo County, largest of its type known in Iowa, and the largest and highest quality bur oak savanna-prairie complex known in the state (in Clay County); (see Figs. 3 and 4) were noted in the IR analysis as areas of potentially high quality prairie (or savanna) communities. This was verified by reports from county conservation board officers in both counties during the time of the IR analysis and by subsequent field checks in the 1984 growing season.

In many cases, IR analysis also discovered previously unknown prairies of high quality. For example, a 50 acre (20.2 ha) prairie-pothole complex (Fig. 5) was discovered in the IR analysis of Cerro Gordo County. Isolated along dirt roads in a heavily farmed area, this prairie had been completely unknown. In fact, upon completion of the 1984 field season, 15 new IR-identified sites were shown to be high quality prairies and an additional 20 previously undocumented IR-identified sites corroborated by secondary reports were shown to be of high quality. This value of air-photo analysis has been proven in Illinois, where the combined use of maps and black-and-white aerial photos yielded 290 previously unknown high quality natural community remnants (White 1978), fully 42% of the total. Without use of such methods, coupled with aerial surveys and field visits, 50% of Illinois' remnant prairies would have been overlooked (White 1981).

The combination of IR photo analysis, secondary source field reports, and staff field inspections has indicated that particular cultural and topographic factors have led to the persistence of most prairie remnants in Iowa. By far the most important factor is steep topography. This is true even in landform regions other than the Loess Hills and Paleozoic Plateau. Steep slopes in stream-dissected landscapes of Iowa, especially along the major rivers and their primary tributaries, are often used for livestock pasture, as it is not economical to plow them. The prairies shown in Figs. 3 and 4 are excellent examples of this situation. Infrared analysis showed the highest concentration of such potential prairie remnants along the upper Little Sioux River (Fig. 6) and its tributaries in northwest Iowa in the Des Moines Lobe and Northwest Iowa Plains landforms. Many of these "prairie pastures" are relatively large (over 30 acres; 12 ha) and contain bur oak savannas (as in Fig. 4). A similar result was obtained in the Illinois Natural Areas

FIG. 5. 50-acre prairie-pothole marsh complex, hayed annually; discovered first by infrared photo analysis in Cerro Gordo County, Iowa.

Inventory, where, with the exception of railroad right-of-ways, "land too steep to plow" was the principal reason given for persistence of a black-soil prairie remnant (White 1978).

On level ground that would otherwise be cultivated, prairie remnants persist in Iowa for 4 major reasons. First, small remnants, generally under 5 acres (2 ha), remain as "odd corners" of land, isolated from cropland by the intersection of transportation corridors (roads and railroads). Some abut cropland on one side, but form the point of a triangle too small to plow or too wet to drain economically. These remnants can be very high quality virgin prairies.

Secondly, portions of, or even entire, cemeteries, unused or little used for burials, frequently harbor prairie remnants of very high quality, though always small (less than 5 acres; 2 ha). During the 1984 field season, 5 high quality cemetery prairies were discovered and inventoried. The IR photo analysis found numerous additional potential cemetery prairies, with an especially high concentration in Lyon County (northwesternmost county in Iowa); most have not been field checked.

Level prairies also persist frequently in Iowa in association with wetlands. Most of the large marsh complexes are state-owned wildlife management areas. Prairies have been reported occurring on the fringes of these marshes, but preliminary indications are that most of these prairies were heavily grazed prior to state acquisition and so are not of high quality. Scattered isolated small potholes surrounded by cropland were discovered by IR analysis; some of these appeared to have prairies fringing them. Shallow upland drainageways and spring-fed swales in eastern Iowa's Iowan Surface landform often have sedge meadows bordered by wet to mesic prairie. Field checks to date have found that only a few of these prairie remnants are undamaged by livestock grazing.

Finally, prairies on arable land in Iowa have persisted due to the cultural tradition of harvesting wild hay (Fig. 5). To date, 35 prairie hayfields of high quality have been identified and field inventoried in Iowa. Fewer than 5 of these are on such moderate slopes that they may also have persisted as pastures, but even these are not too steep to plow. Fourteen high quality prairies are known in Iowa on level to gently rolling (arable) terrain exceeding one quarter-quarter section in size (40 acres; 16.2 ha). All of these sites persisted because they were, or still are, used as hayfields. All 7 of the large ($>$ 40 acres; $>$ 16.2 ha) high quality prairie pothole complex remnants in which prairie (rather than wetland) is the dominant community are, or were, used as hayfields. It is safe to say that, in the absence of a tradition of harvesting wild hay, there would be no large prairie remnants remaining in Iowa on arable land, and certainly no large remnants to represent the southern, or Iowan, portion of the prairie pothole region. A similar situation exists in Minnesota and Missouri. In Minnesota, most remnant prairies lie in the bed of glacial Lake Agassiz in the northwest part of the state (Searle and Heitlinger 1980). Many of these remnants are greater than or equal to a quarter section (160 acres; 65 ha) and persist because prairie haying replaced intensive agriculture in this cool climate region. In Missouri, nearly all large remnant prairies are located in the southwest and west central parts of the state, where the generally (but not exclusively) thin soils on this unglaciated landscape slowed the tide of converting marginal land to row crops. Prairie haying was instead the traditional form of land use (Christisen 1972). In Illinois, the haying tradition either never developed or died out early in the history of settlement. The only high quality prairies remaining on flat or gently rolling land in Illinois today, which are comparable in size to those in Iowa, Minnesota, and Missouri,

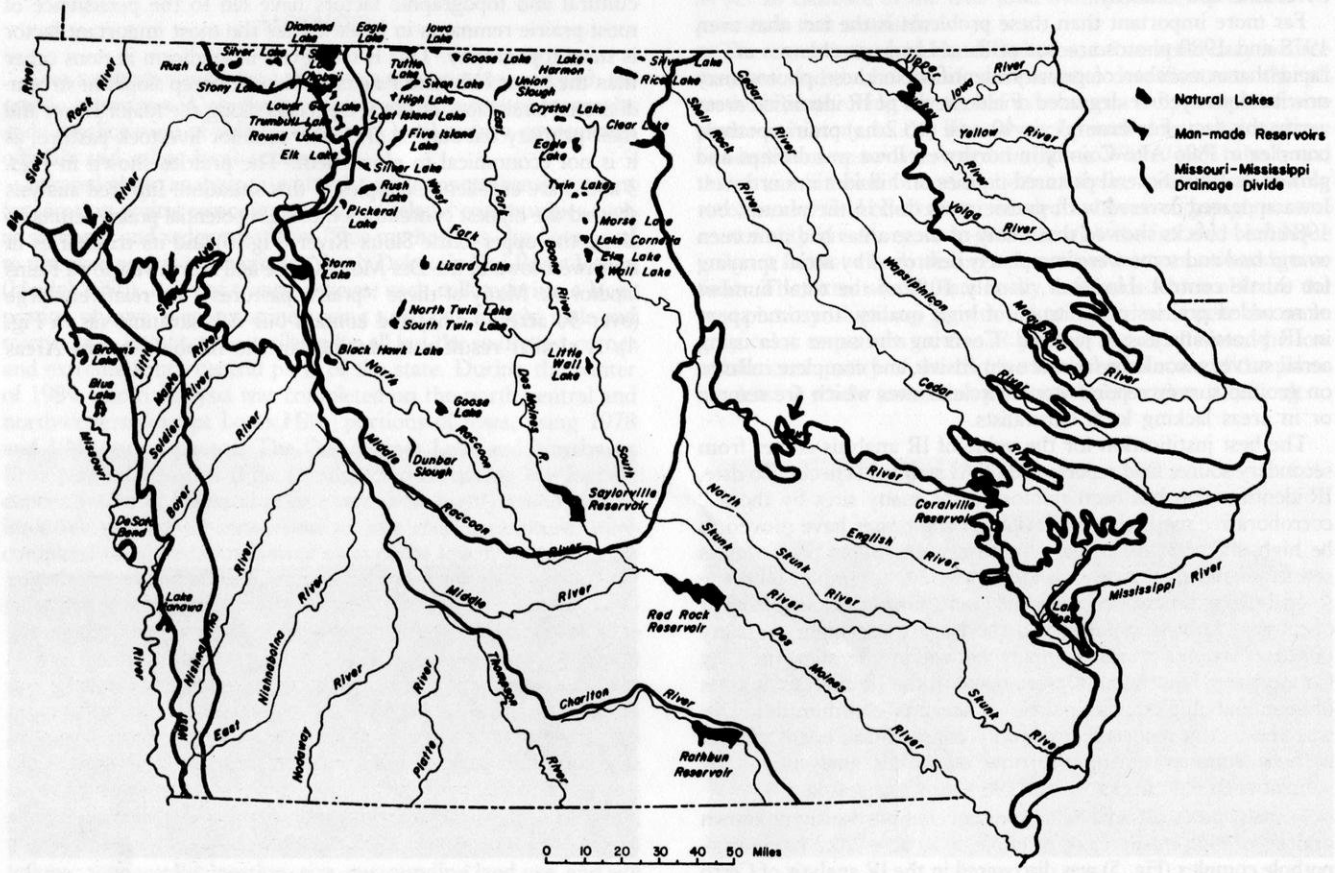

FIG. 6. Rivers and lakes of Iowa (from Prior, 1976).

are on shallow or sandy soils unfit for plowing or on lands once platted for development in Chicago's suburbs (White 1978). In fact, of the tallgrass prairie states having active statewide prairie inventories, Iowa may be unique in that a cultural tradition of haying alone, irrespective of climate and soil type, is responsible for the persistence of large prairie remnants on arable land.

Prairie hayfields in Iowa are traditionally harvested in August, during the period of peak growth and flowering of prairie grasses and many forbs, but after that for cool season Eurasian species. This procedure, repeated annually for several years, has selected for the Old World invaders (especially perennials such as brome and bluegrass) and against the natives, causing a slow but gradual shift from prairie to Eurasian meadow. This trend is further augmented by the fact most Iowa hayfields have been "enriched" by the disking in of familiar cool season Eurasian species such as timothy, red clover, redtop, and Hungarian brome. Because 9 of the 14 large prairie hayfields in Iowa (and many of the smaller ones) are in private ownership and still being hayed, their future is in jeopardy unless the haying schedule can be shifted to fall; or unless management by controlled burning, rather than haying, is instituted, in lieu of outright purchase for conservation purposes.

The prairie inventory in Iowa as of the end of 1984 indicates that prairie remnants in the state are not uniformly distributed as to geographic location or natural community type, as is also true in the neighboring Prairie Peninsula states of Illinois (White 1981), Missouri (Christisen 1972), Minnesota (Searle and Heitlinger 1980), and Wisconsin (Curtis 1959). Compared to their presettlement frequency and acreage, Loess Hills prairies are the best represented of all prairie types. The largest tracts of prairie remaining in Iowa lie on this landform. Discounting a single site of nearly 3,000 acres, there are 20 documented high quality Loess Hills prairie remnants, ranging from 5 to 640 acres (2 to 259 ha) and averaging 125 acres (51 ha). Many of these prairies are, however, threatened by succession to shrubby bur oak woodland because of fire exclusion. While the inventory of hill prairies of the Paleozoic Plateau has just begun, preliminary indications are that remnants of this community are also well-represented, though much smaller, averaging under 10 acres (4 ha). An intensive inventory of hill prairies has been conducted only along the western part of the Upper Iowa River (Fig. 6), but 18 high quality remnants have now been documented in this single region alone. However, as in the Loess Hills, years of fire exclusion are leading to extensive invasion by woody plants, especially red cedar (Blewett 1986).

The inventory of prairie types with a distribution naturally restricted by geologic or topographic criteria is only in its initial stages. Fewer than 6 examples each of high quality limestone prairies (all on the Iowan Surface) and gravel prairies have been documented; more can be expected. Only a single high quality floodplain prairie is known to exist. Additional remnants will be extremely rare because of the high agricultural value of bottomland soils. Known sand prairie remnants in Iowa are restricted to the Lake Calvin basin and dune ridges along the Skunk and Cedar Rivers (Fig. 6), as well as some Mississippi River low sand terraces. But, as of 1984, very few high quality remnants have been discovered; intensive livestock grazing appears to have been practiced on most of Iowa's sand prairies.

The two prairie types which formed the dominant vegetation of most of presettlement Iowa were the blacksoil and clay loam communities. Although location of examples of the clay loam type has depended mostly on irregular field sightings, rather than the more comprehensive infrared photo analysis, there is little doubt that there is an extremely inequitable distribution of remnants both between and among these two natural communities.

Relative to the northern Iowa blacksoil prairies, southern Iowa's clay loam prairies are rarer, smaller, and average lower in quality. The 1984 natural history foray to Decatur and Ringgold counties on Iowa's south central border discovered only 2 high quality prairie remnants, totaling 5 acres (2 ha). A field check of several sites identified by IR analysis in Appanoose County further east found no high quality remnants at all. On the average, two small high quality clay loam prairies are known from each of the counties in the Southern Iowa Drift Plain. The largest known example is the 25 acre (10 ha) Sheeder Prairie State Preserve in west-central Guthrie County. The IR analysis on this county is complete and indicates that many additional potential clay loam remnants may exist on the exceptionally steep hills in parts of this county. The IR analysis of adjacent clay loam prairie areas does not show this, however. A long history of intensive cattle and sheep grazing, planting of many native grass pastures to cool-season grasses, and the probable high sensitivity to soil compaction/degradation of a prairie on heavy clay soils and subsoils are probable reasons for the rarity of high quality prairies on southern Iowa's dissected Kansan drift. The situation is the same in northern Missouri, where this landform region has few known prairie remnants. In fact, Christisen (1978), in his study of recent (post World War II) prairie chicken distributional changes, has shown a correlation between the loss of these birds in northern Missouri and the loss of tallgrass prairie remnants.

Remnants of Iowa's blacksoil prairies are, by contrast, more common and larger, and higher quality examples make up a much greater proportion of the remnants which exist. However, these remnants are far from being equitably distributed. A very high concentration of remnants exists in the eastern half of the Northwest Iowa Plains region and northwestern portion of the Des Moines Lobe region (Iowa Lakes area shown in Fig. 6). Additional smaller concentrations of remnants occur elsewhere on these landforms (especially along rivers), but these remnants are generally more scattered and far less frequent. Most of the reasons for this distribution have been discussed earlier. To these reasons could be added the more rugged and complex glacial topography of this area, its poor drainage system development, and a late date of settlement, the latest in Iowa. With the exception of the latter, this same geological scenario is partly responsible for the concentration of Illinois' blacksoil prairie remnants in the northeast part of that state (White 1978). Although IR analysis has only begun for the third landform region of Iowa with blacksoil prairies, the highly eroded Kansan drift of the Iowan Surface (Prior 1976), this initial analysis, secondary source field sightings, and INAI field checks indicate that these blacksoil prairies are relatively infrequent, small, and seldom of high quality. However, sedge meadows, some with small blacksoil prairie inclusions, in upland drainageways or swales, as at Williams Prairie State Preserve in Johnson County, appear to be relatively frequent. It is remarkable that Hayden Prairie State Preserve, Iowa's largest blacksoil prairie, 240 acres (97 ha), and of very quality, is located on this landform.

CONCLUSION

The work of the Iowa Natural Areas Inventory through 1984 indicates that prairie remnants in Iowa are far more frequent than expected in this highly agricultural state. The state's growing efforts to protect this prairie heritage, as described by State Ecologist Dean Roosa (1976), should guarantee that representative examples of all of Iowa's prairie communities will be preserved for scientific research and education. As the Inventory's data base expands to cover all geographic regions and prairie communities equally and intensively, preservation efforts should concentrate on the types least protected or most susceptible to human destruction or natural successional degradation. If the trends shown by this study hold true as the Inventory progresses, then the present emphasis on preservation of large Loess Hills tracts and larger blacksoil prairie hayfields will shift to include the best remaining examples of Iowa's hill prairies, black soil slope prairies of the Little Sioux River Valley, and the regionally significant southern Iowa clay loam prairies, among others.

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CHARACTERISTICS AND MANAGEMENT OF MISSOURI'S PUBLIC PRAIRIES

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Abstract. The 37 public prairies in Missouri, totaling about 4,343 hectares, are owned by five different agencies. These prairies, ranging from 1 to 595 hectares, occur mainly in southwest Missouri. Upland, bottomland, and loess hill prairies are protected. The prairies provide important habitat for rare or endangered birds in the state including greater prairie chickens, upland sandpipers, Henslow's sparrows, and northern harriers. In addition, 11 state listed rare or endangered plants occur on public prairies.

The Missouri Department of Conservation manages 30 prairies, with the goal of maintaining the greatest diversity of indigenous species on each one. Management consists of spring burning, summer haying, or periodic grazing, used on a rotational basis. Each technique is used for specific purposes. Invasion of introduced cool season grasses is controlled by spring burning, while middle to late July haying maintains relatively high plant diversity. Light to moderate grazing improves wildlife habitat by diversifying vegetation height and density.

INTRODUCTION

In presettlement times, tallgrass prairie covered approximately 26% of Missouri and encompassed 47,663 square kilometers (Schroeder 1981). Today, less than 30,352 hectares of prairie remain (Christisen 1972), and most of it is confined to southwest Missouri. Since 1957, the Missouri Department of Conservation, The Nature Conservancy, the Missouri Prairie Foundation, the Missouri Department of Natural Resources, and the University of Missouri have purchased 37 native prairies, which occur mainly in southwest and west-central Missouri (Fig. 1).

CHARACTERISTICS

Missouri's public prairies are broadly classified into two types, upland and bottomland prairies. Upland prairies occur on nearly level to hilly areas with soils derived from loess, sandstone, shale, cherty limestone, or dolomite (Anderson 1979). The vegetation is dominated by tall and medium height warm season grasses including big bluestem, little bluestem, Indian grass, switchgrass, panicums, and dropseeds (Drew 1947, Kelting 1982). A large variety of forbs are present, with an average of over 200 vascular plant species found on many areas. One of the largest public prairies, Taberville Prairie, has over 400 vascular plant species (Toney 1980).

Upland prairies can be subclassified into shallow soil uplands, deep soil uplands, and loess hill prairies. Shallow soil upland areas have shallow, well drained soils which usually vary from 0 to 48 cm deep and typically occur on ridgetops and south or west slopes (Toney 1982). The vegetation is dominated by bunch grasses,

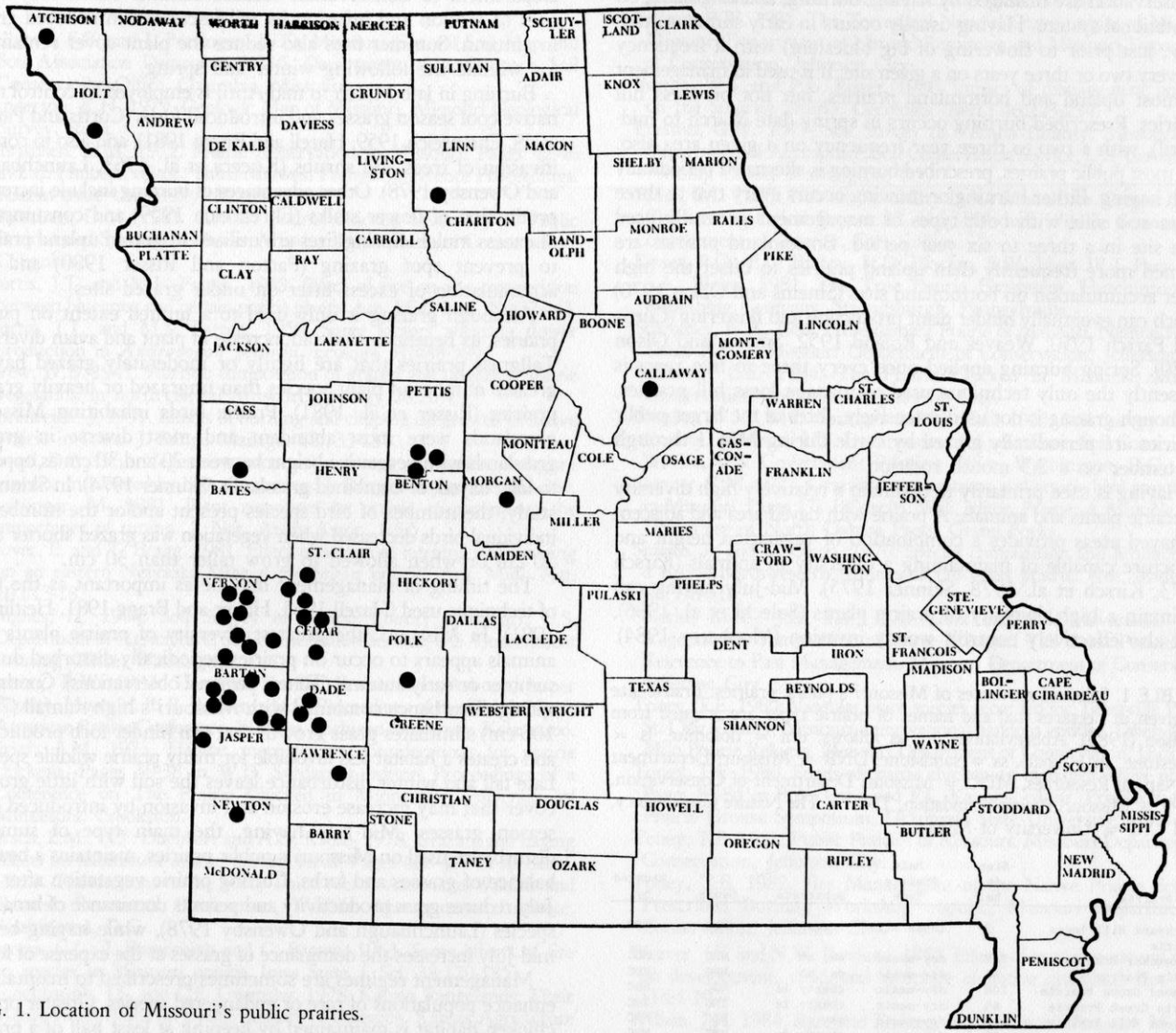

FIG. 1. Location of Missouri's public prairies.

composites and legumes, with shrubs and trees scattered on rockier sites. These sites have relatively low vegetative production compared to the other prairie types. Deep soil uplands, with soils typically from 48 to 144 cm or more in depth (Hughes 1974, Preston 1977), maintain greater moisture than shallow soil uplands. Vegetation consists of sod and bunch grasses, with numerous forbs and few shrubs or trees. Plant litter accumulates at a faster rate than on shallow soil uplands.

Loess hill prairies occur on steep south or west slopes and ridgetops of dissected hills with well drained, loamy soils (Nelson 1985). Loess deposits underlying these prairies range from 3 to 28 meters or more in depth (Shrader et al. 1953). Both tallgrass and shortgrass prairie plants are present, including little bluestem, Indian grass, sideoats grama, buffalo grass, and hairy grama grass (Nelson 1985).

Missouri's public prairies, ranging in size from approximately 1 to 595 hectares (Toney 1981), include 31 dry-mesic upland prairies, 4 bottomland (wet) prairies, and 2 loess hill prairies (Table 1). Of the 4,343 hectares of prairie currently protected in the state, about 90% of this is upland prairie. The four wet prairies total 393 hectares, while the two loess hill prairies comprise nine hectares.

These public prairies harbor six animals listed as rare, endangered, or status undetermined in the state, including four birds, one mammal, and a fish (Wilson 1984). These are the greater prairie chicken (*Tympanuchus cupido*), northern harrier (*Circus cyaneus*), upland sandpiper (*Bartramia longicauda*), Henslow's sparrow (*Ammodramus henslowii*), plains harvest mouse (*Reithrodontomys montanus*), and the blacknose shiner (*Notropus heterolepis*).

Furthermore, five state listed rare or endangered plants (Wilson 1984) occur on upland prairies, including pale green orchid (*Habenaria flava*), yellow-eyed grass (*Xyris torta*), Harvey's beakrush (*Rhynchospora harveyi*), Mead's milkweed (*Asclepias meadii*), and arrowhead (*Sagittaria ambigua*). Mead's milkweed, proposed as a federally endangered species, occurs on 10 preserved prairies, with the single largest population known in the United States (over 500 plants) present on one of these prairies. The two public loess hill prairies contain the following six state listed rare or endangered plants (Wilson 1984): skeleton plant (*Lygodesmia juncea*), low milk vetch (*Astragalus lotiflorus*), downy painted cup (*Castilleja sessiliflora*), soapweed (*Yucca glauca* var. *glauca*), wolfberry (*Symphoricarpos occidentalis*), and *Dalea enneandra*.

MANAGEMENT

The Missouri Department of Conservation has three objectives in prairie management. These are: (1) to maintain the highest diversity of prairie species, both plants and animals, native to a given site, (2) to enhance habitat for prairie wildlife, and (3) to protect sites with rare or endangered plant or animal populations.

Public prairies cared for by the Missouri Department of Conservation are managed by haying, burning, and/or grazing on a rotational system. Haying usually occurs in early summer (mid-July, just prior to flowering of big bluestem) with a frequency of every two or three years on a given site. It is used in management of most upland and bottomland prairies, but not on loess hill prairies. Prescribed burning occurs in spring (late March to mid-April), with a two to three year frequency on a given area also. On most public prairies, prescribed burning is alternated periodically with haying. Either burning or mowing occurs every two to three years at a site, with both types of management generally used at a site in a three to six year period. Bottomland prairies are burned more frequently than upland prairies to offset the high litter accumulation on bottomland sites (Smeins and Olson 1970) which can eventually hinder plant production and flowering (Curtis and Partch 1950, Weaver and Roland 1952, Smeins and Olson 1970). Spring burning applied once every three to five years is presently the only technique used to manage loess hill prairies. Although grazing is not used extensively, three of the larger public prairies are periodically grazed by cattle during May 1 through September on a 2.5 month rotation.

Haying is used primarily to maintain a relatively high diversity of prairie plants and animals. A prairie with hayed area and adjacent unhayed areas provides a combination of vegetation height and structure capable of maintaining a diversity of animals (Kirsch 1973, Kirsch et al. 1978, Skinner 1975). Mid-July haying can maintain a high diversity of prairie plants (Solecki et al. 1986), and also effectively controls woody invasion (Mooberry 1984).

TABLE 1. Selected attributes of Missouri's public prairies. Prairie size is given in hectares (ha) and names of prairie types are adapted from Nelson (1985). Abbreviations are as follows: dm = dolomite, ls = limestone, sh = shale, ss = sandstone, DNR = Missouri Department of Natural Resources, MDC = Missouri Department of Conservation, MPF = Missouri Prairie Foundation, TNC = The Nature Conservancy, and UM = University of Missouri.

Prairie	Size in ha.	Main Prairie Type	Substrate	Owner	Managed by
Brickyard Hill Loess Prairie	5	loess hill	loess	MDC	MDC
Bushwacker Prairie	269	dry-mesic	ss, sh	MDC	MDC
Catlin Prairie	60	dry-mesic	ss, sh	MDC	MDC
Diamond Grove Prairie	208	dry-mesic	cherty ls	MDC	MDC
Dorris Creek Prairie	65	dry-mesic	cherty ls	TNC	TNC
Dorsett Hill Prairie	6	dry-mesic	sh	MDC	MDC
Drover Prairie	32	dry-mesic	cherty dm	MPF	MDC
Flight Lake Prairie	22	wet	alluvium	MDC	MDC
Friendly Prairie	16	dry-mesic	cherty dm	MPF	MDC
Gama Grass Meadows	32	dry-mesic	ss, sh	TNC	MDC
Gay Feather Prairie	47	dry-mesic	ss, sh	MPF/MDC	MDC
Golden Prairie	122	dry-mesic	ss, sh, ls	MPF	MPF
Hite Prairie	27	dry-mesic	cherty ls	MDC	MDC
Hunkah Prairie	65	dry-mesic	sh	TNC	MDC
Indigo Prairie	16	dry-mesic	cherty ls	MDC	MDC
LaPetite Gemme Prairie	15	dry-mesic	ss, sh, cherty ls	MPF	MDC
Little Osage Prairie	32	dry-mesic	ss, sh	TNC	MDC
Locust Creek Prairie and Cordgrass Bottoms	316	wet	alluvium	DNR	DNR
Marmaton River Bottoms	45	wet	alluvium	TNC	TNC
McCormack Loess Prairie	4	loess hill	loess	TNC/MDC	MDC
Mo-Ko Prairie	166	dry-mesic	ss, sh, cherty ls	TNC	MDC
Monegaw Prairie	109	dry-mesic	ss, sh, cherty ls	TNC/MDC	MDC
Mount Vernon Prairie	16	dry-mesic	cherty ls	TNC	MDC
Niawathe Prairie	130	dry-mesic	ss, sh, cherty ls	TNC/MDC	MDC
Osage Prairie	564	dry-mesic	ss, sh	MDC	MDC
Paint Brush Prairie	62	dry-mesic	cherty dm	MDC	MDC
Pawhuska Prairie	31	dry-mesic	ss, sh	TNC	MDC
Penn-Sylvania Prairie	65	dry-mesic	ss, sh, ls	MPF	MPF
Prairie State Park	595	dry-mesic	ss, sh	DNR	DNR
Prairie Woods State Forest	8	wet	alluvium	MDC	MDC
Schell-Osage Prairie (6 prairie remnants)	69	dry-mesic	ss, sh, cherty ls	MDC	MDC
Sky Prairie	81	dry-mesic	ss, sh, cherty ls	MDC	MDC
Taberville Prairie	571	dry-mesic	ss, sh, ls	MDC	MDC
Tucker Prairie	59	dry-mesic	loess	UM	UM
Tzi-Sho Prairie	65	dry-mesic	ss, sh	TNC	MDC
Wah-Kon-Tah Prairie	283	dry-mesic	cherty ls	TNC	MDC
Wah-Sha-She Prairie	65	dry-mesic	sh	TNC	MDC

Summer haying is preferred over summer burning by the Missouri Department of Conservation because summer burns may open sites to erosion and invasion by tall fescue (an introduced grass) in autumn. Summer fires also reduce the plant cover remaining for wildlife the following winter and spring.

Burning in late March to mid-April is employed to control non-native cool season grasses and introduced forbs (Curtis and Partch 1948, Ehrenreich 1959, Hazell and Bragg 1981), and also to control invasion of trees and shrubs (Kucera et al. 1963, Launchbaugh and Owensby 1978). Other advantages of burning include increased production of flower stalks (Ehrenreich 1959) and consumption of excess mulch. Spring fires are utilized in grazed upland prairies to prevent spot grazing (Parton and Risser 1980) and the accumulation of excess litter on under grazed sites.

Although grazing is only used to a limited extent on public prairies, its benefits include an increase in plant and avian diversity. Tallgrass prairies that are lightly or moderately grazed have a greater number of plant species than ungrazed or heavily grazed prairies (Risser et al. 1981). Prairie birds inhabiting Missouri grasslands were most abundant and most diverse in grazed grasslands with vegetative height between 20 and 30 cm as opposed to idle, hayed, or combined grasslands (Skinner 1974). In Skinner's study, the number of bird species present and/or the number of individual birds decreased when vegetation was grazed shorter than 20 cm or when allowed to grow taller than 30 cm.

The timing of management may be as important as the type of technique used (Hazell 1965, Hover and Bragg 1981, Heitlinger 1981). In Missouri, the greatest diversity of prairie plants and animals appears to occur on prairies periodically disturbed during summer or early autumn (Toney, personal observations). Continued spring disturbance combined with Missouri's high rainfall (76 to 106 cm) stimulates grass growth that can hinder forb production and creates a habitat less favorable for many prairie wildlife species. Late fall and winter disturbance leaves the soil with little ground cover that may increase erosion and invasion by introduced cool season grasses. Mid-July haying, the main type of summer disturbance used on Missouri's public prairies, maintains a healthy balance of grasses and forbs. Cutting prairie vegetation after late July reduces grass productivity and permits dominance of broadleaf species (Launchbaugh and Owensby 1978), while haying before mid-July increases the dominance of grasses at the expense of forbs.

Management regimes are sometimes prescribed to maintain or enhance populations of rare or endangered species. Greater prairie chicken habitat is maintained by keeping at least half of a prairie in prime nesting habitat (Schwartz 1944, Kirsch 1973, Prose 1985). According to Prose (1985), greater prairie chickens prefer to nest on areas with vegetation between 20 and 40 cm tall, rather than on areas with shorter or taller vegetation. At each public prairie inhabited by prairie chickens, at least 50% of the prairie is hayed in mid-July, with haying site alternating from year to year on each prairie. In spring, management units which were idle (unhayed) the previous year have plant cover within the height preferred by prairie chickens. A 1981 census (Christisen 1981) showed that the greatest number of prairie chickens occured on public prairies managed by haying once every two to three years. This management system also maintains a diversity and abundance of forbs used for food and for raising broods. Prairie chicken broods prefer prairies rich in broadleaf plants (Prose 1985). Prairie chickens studied on managed prairies in Missouri relied heavily on native plants for food, with 71% of their diet composed of native plants (Toney 1980). Upland sandpipers prefer grazed grasslands with vegetation height between 10 and 30 cm to idle or hayed grasslands (Skinner 1975). As a result, several of Missouri's public prairies are periodically grazed to provide preferred habitat for these rare birds. Populations of rare or endangered plants are maintained by mid-July haying every two or three years. All known populations of rare or endangered plants on public prairies are maintaining themselves or increasing under this management regime.

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WHY BOTHER TO PROTECT PRAIRIES ALONG RAILROADS?

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Abstract. Railroad rights-of-way serve as prairie refuges. Railroads harbor the only prairie vegetation in large parts of the Prairie Peninsula. For example, the only natural black-soil prairie remnants in 12 Illinois counties are along railroads. Prairie is more abundant as rangeland farther west, but many kinds of prairie have been so generally degraded by grazing that railroads provide some of the best evidence of species composition in the absence of overgrazing. Railroads provide long cross-sections of diverse soil and vegetation types. They are places to study prairie soil, plants, and animals; and they serve as models and seed sources for prairie restorations. Many railroad prairies have maintained a high native plant species diversity even though the remnants are often small, narrow, and discontinuous. This indicates that they can be managed as viable and defensible preserves. Many railroad prairies are endangered by brush encroachment, railroad maintenance, and railroad abandonment. They deserve priority for protection.

Small prairie remnants have persisted on railroad rights-of-way. Why is it important to protect them? The commonest response to this question is, "That's all we have." In some regions, the only prairies are along railroads because the tracks were laid across the prairie before it was farmed. This answers the basic question, but I will share a few other ideas. I want to pursue this "Why bother?" question a bit more.

Preservation of railroad prairies is justified with the same purposes that justify protection of any kind of natural feature, such as education, research, aesthetics, and moral obligations. The reasons most often cited for nature preserves are (1) maintenance of natural ecosystems, (2) maintenance of natural diversity, and (3) protection of rare species. Railroad prairies are important remnants of ecosystems, and they are important refuges for prairie species.

Preserving species is important, but we should not make a mistake by putting too much emphasis solely on species conservation. I have seen a steady change in focus in the nature preservation movement in my short career. Ten years ago I thought nature preservationists were in the business of preserving natural diversity, or nature that encompasses more than plants and animals (stalactites, for example). Then we started talking more and more about the preservation of ecological diversity (forget the stalactites); then we emphasized biological diversity (forget the caves unless they provide habitat for rare species). Now people are joining the preservation movement who think that the only business is preservation of genetic diversity: genes, not even plants or animals.

Genetic engineers are making so much progress that we may need to come up with another excuse for nature preserves, other than maintaining genetic diversity. If we are so interested in genetic diversity, perhaps we should invest in recombinant DNA labs instead of investing in land.

A smart man has said that the first rule of intelligent tinkering is to save all the parts. (That is, save the species.) Another rule might be as important: before tinkering, set aside a working model. (That is, save the ecosystems.)

Even if one thinks that protecting prairies is important (either as ecosystems or as species habitats), one might question whether small remnant prairies along railroads are worth protecting. They are. In many regions, they are all we have. These prairies are small and beat up, but we do not discard classic works of art just because they have deteriorated from time, war, or floods. They can be restored; or even if they cannot be restored, we still keep them. We admire Venus de Milo though she has no arms.

Some persons think that small railroad prairies will gradually deteriorate to the point where even I will not want to protect them. We should save some and find out, not give up on them now. The current fad of island biogeography theory has provided many good ideas about how to select and design nature preserves, but uncritical acceptance and application of those theories is doing disservice to nature when it leads one to conclude that we should not bother to protect small prairies. Bison no longer course through railroad prairies – the fauna may be a shambles – but the vegetation has not necessarily followed suit. Any tenth-acre patch of prairie isolated along a railroad is apt to have roughly the same native vascular plant species composition as any tenth-acre patch randomly selected in any 100 or 300-acre prairie. These railroad prairies are not falling apart as fast as one might assume. They have been isolated in cropland for a hundred years, and the fact that we are still talking about them – the mere fact that railroad prairies still exist – is telling. It tells us that they are viable.

To help clarify what we should protect along railroads, consider two kinds of railroad prairie: (1) little, high quality, relatively undisturbed ones, and (2) bigger, more degraded ones. There are no big good railroad prairies. This poses a classic dilemma. Should we protect the small, high quality remnants with relatively undisturbed vegetation; or do we work to save the bigger, more degraded ones because they have potential to be restored and because they might provide better habitat for some animals? The answer: we do both.

Often it is not easy to set aside the small, high quality railroad prairie remnants because they are few and far between. There are few choices and sometimes they occur where preservation is difficult, but we should focus on them first. We should not delay preservation efforts just because we have not finished inventories to find all the railroad prairies. The best remnants are obvious, and every one of the best merits attention. We also need to protect long stretches, miles and miles of weedy prairie, especially where they connect smaller patches of high quality prairie.

A series of small, high quality prairies interspersed between long stretches of degraded vegetation gives the best opportunity for (1) maintaining species diversity, (2) buffering the high quality sites, and (3) restoring the degraded areas with local ecotypes. In some places it should be possible to buy adjacent farmland and then stop farming right next to the prairie. This would provide a buffer strip against herbicide drift and would make room for restoration. As the prairie spreads away from the tracks, a wider and wider strip could be removed from cultivation over the years.

Conservation groups often find that negotiating protection and then managing a few acres require roughly the same resources as needed for a site several times as large. A railroad company may be more apt to agree to protect a long stretch of prairie (between road crossings, for example) rather than to watch out for several small, isolated patches on the same right-of-way. One should not set limited goals by assuming that the difficulty of protecting a railroad prairie is in exact proportion to its length.

The long, narrow railroad rights-of-way often encompass a cross-section of soil types and vegetation types, which is nice. Also, the cuts and fills along the railroads have created artifically wet or dry places, which harbor native species that could not otherwise find refuge along the track. The railroad prairies also serve as travel and dispersal corridors for plants and animals. They are not sources of weeds for adjacent farm fields: that can be easily proven.

I come from the Prairie Peninsula, where prairie is essentially exterminated. There are more tall-grass prairies west of the Mississippi but you are deluded if you think all those great big pastures in the Flint Hills of Kansas have natural prairie vegetation.

Railroads have some of the very few places where tall-grass prairie has not been damaged by livestock or haying, even in the center of the tall-grass prairie region. In the eastern Prairie Peninsula, native prairie is very prone to invasion by woody plants, and it is quickly replaced by exotic grasses and weedy native forbs if the soil is disturbed or if the vegetation is grazed. Farther west, prairie is more likely to persist, in part because the native plants are much better adapted to grazing. However, tall-grass prairie is not the only grassland type where railroads harbor a significant part of the natural remnants.

When ecologist Rexford Daubenmire studied Pacific Northwest grasslands in the 1960's, he visited railroads and cemeteries because he could find so few undisturbed areas of certain habitat types. Think of it: he had to resort to cemeteries and railroads to find native vegetation on undisturbed soil. Other scientists have done the same: I know of over 50 papers that are either based on studies along railroads or that emphasize the importance of railroads as prairie refuges. Many of Daubenmire's study plots have been lost, but some can still be found - sometimes along a railroad. Though railroads have served as prairie refuges for over a century, we cannot assume that these prairie remnants will persist without deliberate protection and management.

I will emphasize this point by recounting experiences of the Illinois Natural Areas Inventory (White 1978). This project used aerial surveys to find railroad prairies in the fall of 1975. Inventory biologists saw three stands of prairie grass being bulldozed as they flew over them; two more were plowed or bulldozed before they could be visited the next day; a sixth site was destroyed within 2 weeks of being spotted from the air. Although all these sites might not have proven to be high quality prairie, they were destroyed faster than they could be surveyed. After the aerial searches and preliminary on-the-ground checks of each site, 64 remnants were selected as natural prairies; yet 4 of these were destroyed before they could be revisited the following summer. The Illinois Department of Conservation has made some effort to try to ensure that the remaining railroad prairies receive protection, and there have been some successes. However, of the 24 prairies identified along northwestern Illinois railroads in 1976, 5 were completely eliminated and 7 had been partly destroyed or severely damaged by 1984.

Soldiers wounded in battle are sometimes put in three groups. Some soldiers are apt to survive without medical treatment; some are expected to die no matter what help they might get; and some will die unless they are treated immediately. Railroad prairies fall into this third group. We can save them but they must be saved. They will not persist indefinitely without protection because they are being destroyed.

We can do better than medical doctors on the battlefield. We can "raise the dead." We can restore prairies, recreate them; railroad prairies are very valuable as sources of seed and as models for these efforts.

We should be careful not to put too much emphasis on planting new prairie vegetation or restoring degraded prairies if this is at the expense of protecting the few relatively undisturbed remnants. After one starts protecting and managing a prairie, there are rapid improvements for perhaps 3 to 5 years and then more gradual changes for 10 years and longer. With enough time and care, one can establish a good stand of grass and increase the other native species in a degraded prairie, but some forbs and animals will not reestablish their numbers without help because they simply are no longer present. This makes the few relatively diverse remnants all the more important. High quality examples of the commonest tall-grass prairie types are just as rare and endangered as disturbed examples of the rarer community types.

We must protect prairies in every state and region. There are thousands of acres of prairie in southwest Missouri, and thousands of acres have been protected; but that does not mean that we should not bother to protect railroad prairies in Illinois. As a general rule, people have exploited the land about as much as they can, and the fact that there are many prairies in Missouri but hardly any in Illinois indicates that the prairies differ. The prairies remaining in Missouri are, for the most part, on shallow, rocky soil. The ones in Illinois were on deep, loamy soil, so they were essentially all plowed. To protect the full diversity of prairie communities, we need to protect Missouri prairies as well as what remains in Illinois, much of it along railroads.

In 1978 Illinois workers completed a state-wide survey of all types of prairies, and I understand that they did a thorough search (White 1978, 1981, Bacone and Harty 1981). They found 641 acres (about 1 square mile) of natural black-soil prairie on fine-textured soil in the entire state. They found a total of 2,352 acres (less than 4 square miles) of natural prairie on all soil types; 123 acres were along railroads in 60 patches, along 12,000 miles of track. Railroads harbored the only black-soil prairie remnants in 12 counties. About one-third of the 102 Illinois counties have no undisturbed prairie, even along railroads. One might question whether it is smart to try to protect one-quarter to 4-acre remnants along Illinois railroads, but look at it this way: if we save a 2-acre patch of prairie, the only prairie in a county, then in one sense we have saved "a county's worth" of original prairie.

When I reported these statistics about Illinois prairies at the 1978 North American Prairie Conference, I said we should be crying for shame; and some of us did cry. A few weeks later I spoke to the beginnings of the Natural Areas Association and said we should quit crying and get to work, and some of us did go to work. We have accomplished a lot; we have lost a lot, too. We need to do a lot more and we can do a lot more. Tall-grass prairie remnants are precious, and it is a disgrace to continue to lose them.

I have been told that the next 10 years is all the time we have to protect what remains of our natural heritage. You have probably heard this too– I have been hearing it for about 20 years! Ten years from now we will be repeating the phrase. In the case of railroad prairies, I am afraid that this prediction may be too close to the truth. Destruction of railroad prairies is increasing. One pass with a railroad car spraying herbicide can permanently damage a prairie, and a crew can cover miles of track in a day. We are also losing prairies as the railroads are abandoned. Railroad prairies are disappearing faster than other kinds of prairies. We cannot save everything so we must set priorities. We should give priority to protecting railroad prairies because if we do not do it now we will not be able to do it later.

I have made some statements in part just to catch your attention. If you find some of my assertions outlandish, I hope you have an open mind. You might change your mind or make up your mind later, but we do not have a lot of time. Lest my rhetoric has obscured some points, I repeat: preserving endangered species is important; preserving undisturbed ecosystem remnants is also important; restoring degraded communities is important; and so is protection of large areas of disturbed native habitat for common species. We need to do all these things, none exclusively at the expense of others. Remember diversity.

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MISSOURI'S PRAIRIE DAY: A TARGETED INTERPRETIVE EVENT

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Abstract. In 1983 and 1984, the Missouri Department of Conservation specifically targeted its annual Prairie Day interpretive event toward a local landowner audience. The events were held near the heart of Missouri's remaining 32,400 ha (80,000 acres) of prairie.

We wanted landowners to learn about prairie and native grasses in an enjoyable atmosphere, to appreciate that prairie has vanished from most of the state, and, ultimately, to protect their own prairie land and to establish native grasses.

The usual interpretive programs were supplemented with presentations on native hay and pasture management and grass establishment, special walks for landowners, and a display showing remaining prairie in the thirteen-county area. Publicity targeted local farmers, especially those owning prairie.

Analysis of participant evaluation cards showed about 40 percent of 320 respondents farmed or owned farm land, and about 20 percent of these owned native prairie. Total attendance for both one-day events combined was about 725. All landowner respondents felt they learned something about prairie, and 79 percent thought they learned "quite a bit." Ninety-five percent rated Prairie Day "very enjoyable" or better. The non-landowner participants rated their enjoyment and amount of knowledge gained similarly to the landowners.

INTRODUCTION

Since 1980, the Missouri Department of Conservation has been holding special Prairie Day interpretive events to promote the appreciation and conservation of Missouri's prairie resources (Maupin et al. 1982). In addition to attracting the public at large, the 1983 and 1984 Prairie Days were designed to draw local landowners, many of whom own prairie. We hoped to influence the attitudes and actions of the people who control most of the state's remaining prairie. About 85% of Missouri's 32,400 ha (80,000 acres) of prairie is privately owned. In addition to encouraging public support for prairie preservation, our goal has been to promote good prairie management by private landowners. Recent Prairie Days have, in this respect, been an effort to use interpretation as a management tool (Sharpe and Gensler 1978).

This paper describes the Prairie Day program and discusses the emphasis on local landowner participation of the past two Prairie Days. It also presents results of participant surveys that we conducted at these events.

FIG. 1. Naturalist-guided walks with small groups formed the core of the Prairie Day interpretive program. Walks ended at a tipi with a living history demonstration. Photo by Robert Venner.

DESCRIPTION OF EVENT

Prairie Days are large-scale, organized, well-publicized, one-day interpretive events designed to raise public awareness of Missouri's prairie resource. We held the seven Prairie Days on three public prairies (Diamond Grove, Niawathe and Paint Brush) in southwestern Missouri, where Missouri's remaining prairie occurs.

THE DAY'S ACTIVITIES

A typical Prairie Day begins at 8:00 a.m., and some of the activities are illustrated in Figs. 1-4. The people working Prairie Days are mostly volunteers from both Department staff and from outside the agency. Prairie Day workers are given instructions several weeks before the program.

Arriving visitors are greeted at a central information table. Pick-up trucks, tables, or other displays on various subjects flank the information table. For the mammal talk, mounted specimens are used as props for discussion and examination by participants. We let people touch the specimens. Live small mammals are sometimes trapped on the prairie for display. The bird talk props consist of mounted prairie birds and museum skins. Ornithologists in charge of the talk sometimes mist net and band birds as part of the program. Some prairie birds can be seen or heard during most of the presentations.

Herpetologists use photographs and live animals to show people frogs, toads, salamanders and reptiles native to tallgrass prairie. Children especially seem to enjoy touching and holding the snakes. A live six foot bullsnake is always a popular attraction.

"Living history" programs supplement the tailgate talks. In addition to showing the importance of prairie to American cultural development, these programs focus attention on the dramatic disappearance of prairie in the last 150 years. At one station women dressed in 1850's garb speak of the pioneers and the settlement of the prairie. They discuss their experiences traveling with a wagon train, building and living in a sod house and surviving prairie fires and blizzards. Other living history exhibits have included a drovers' camp (complete with cowboys and chuckwagon), a public land survey crew, and a fur traders' lodge. Tailgate talks and living history presentations last from 30 minutes to one hour.

Naturalist-led prairie walks form the core of the interpretive effort. Walks leave throughout the day with groups of up to 20 participants in each tour. The walks last about one hour and fifteen minutes. Naturalists talk about plants, animals and other features encountered on their walks, and tailor their presentations to the age and interest level of their groups. We emphasize ecological concepts rather than details such as plant and animal identification. Tour leaders address the disappearance of the tallgrass prairie near the conclusion of their walk. Walks end at a tipi occupied by "fur traders" of the early 1800's. In contrast to the 20th Century naturalists, the traders talk of the prairie as a wasteland between St. Louis civilization and "the Shining Mountains" - a wasteland, they insist, where only Indians and buffalo can ever survive. The contrast of the trappers' view of prairie with the modern reality had emotional as well as intellectual impact. At the end of the naturalist tours we invited people to explore and enjoy the prairie on their own.

TARGETING AN AUDIENCE

We modified the publicity and program for the last two Prairie Days specifically to attract local landowners, particularly those who own unplowed prairie. We saw Prairie Day as an opportunity for landowners to learn more about prairie and native grasses in an enjoyable atmosphere, to appreciate that prairie has vanished from most of Missouri (even though it may seem common in their area), and, ultimately, to motivate them to protect their own prairie land and to establish native grasses. We did not reduce publicity toward the larger non-landowner audience, nor did we

FIG. 2. A large map display showed the extent of presettlement prairie and the location of prairie remnants in the region. Landowners could locate their own farms and place them in the context of prairie distribution. Photo by Richard Thom.

FIG. 3. A plains Indian tipi occupied by traders of the early 1800s was the background for discussion of Indian life and the early historical period. Photo by Robert Venner.

TABLE 1. Selected Combined Results of 1983 and 1984 Prairie Day Participant Evaluation Survey. (There were 327 respondents, but N varies from question to question because not all questions were applicable to all respondents, and because some respondents did not answer all questions.) Multiple answers were possible for some questions.

Reasons for Attending Prairie Day (Multiple responses were possible)

Reason	Number	Percent
See prairie wildflowers	239	71
See prairie wildlife	203	60
Photography	39	12
Have family outing	99	29
Get together with friends	47	14
Group outing	85	25
Just curious	79	23
Other	39	12

Number of Respondents Who Farm or Own Agricultural Land in Missouri

Farm or Own Land	Number	Percent
No	191	60
Yes	129	40

Number of Agricultural Landowners or Farmers with Native Prairie on Their Property

	Number	Percent
No native prairie	91	80
Have native prairie	23	20

Respondents' Knowledge of Prairies Before Prairie Day, by Whether or Not Respondent Owns or Farms Agricultural Land in Missouri

	Does Not Farm or Own Land		Does farm or Own Land	
Prior Knowledge	Number	Percent	Number	Percent
Very little	62	33	32	25
Some	97	52	74	59
Quite a bit	29	15	20	16

Agricultural Landowners' Knowledge of Prairies Before Prairie Day, by Whether or Not Landowners Have Native Prairie on Their Property

	Have no Prairie		Have Prairie	
Prior knowledge	Number	Percent	Number	Percent
Very little	27	30	3	14
Some	51	57	13	59
Quite a bit	12	13	6	27

Amount Learned by Participants at Prairie Day

Amount	Number	Percent
Very little	2	Less than 1
Some	71	22
Quite a bit	252	77

Amount Learned by Participants at Prairie Day, by Amount of Participants' Prior Knowledge of Prairies

	Very Little		Some		Quite a Bit	
Prior Knowledge	Number	Percent	Number	Percent	Number	Percent
Very little	1	1	16	16	80	82
Some	0	0	34	19	146	81
Quite a bit	1	2	26	50	25	48

Amount Learned by Participants at Prairie Day, by Whether or Not Participant Farms or Owns Agricultural Land in Missouri

	Does Not Farm or Own Land		Does Farm or Own Land	
Amount Learned	Number	Percent	Number	Percent
Very little	2	1	0	0
Some	40	21	27	21
Quite a bit	146	78	99	79

Amount Learned by Farmers and Agricultural Landowners at Prairie Day, by Whether or Not They Have Native Prairie on Their Property

	Have No Prairie		Have Prairie	
Amount Learned	Number	Percent	Number	Percent
Very little	0	0	0	0
Some	20	22	6	27
Quite a bit	70	78	16	73

Participant Enjoyment of Prairie Day

Enjoyment	Number	Percent
Not enjoyable	0	0
Slightly enjoyable	14	4
Very enjoyable	196	59
Most enjoyable	124	37

Participant Enjoyment of Prairie Day, by Whether or Not Participant Farms or Owns Agricultural Land in Missouri

	Does Not Farm or Own Land		Does Farm or Own Land	
Enjoyment	Number	Percent	Number	Percent
Not enjoyable	0	0	0	0
Slightly enjoyable	7	4	7	5
Very enjoyable	110	58	79	63
Most enjoyable	72	38	40	32

Farmer and Agricultural Landowner Enjoyment of Prairie Day, by Whether or Not They Have Native Prairie on Their Property

	Have No Prairie		Have Prairie	
Enjoyment	Number	Percent	Number	Percent
Not enjoyable	0	0	0	0
Slightly enjoyable	7	8	0	0
Very enjoyable	57	63	16	73
Most enjoyable	26	29	6	27

FIG. 4. Pioneer women told stories about the settlement of the prairie in a living history program that was especially geared to children. Photo by Robert Venner.

eliminate any of the programs that had proved popular with our usual audience. We viewed our pitch to local landowners as an ancillary effort, and considered any positive results to be a kind of program bonus - achieved with just a little additional effort and expense.

Realizing that farmers must be given economic as well as aesthetic incentives to preserve prairie, we supplemented our usual interpretive programs with presentations on native hay meadow and pasture management, special tours for landowners, a display showing remaining prairie in a thirteen-county area, and literature on prairie management for farmers and ranchers.

To attract local landowners, a special effort was made to get publicity in small local papers and on rural radio stations. We wrote an article on prairie and its agricultural uses for the *Missouri Ruralist*. This popular agricultural magazine ran sidebar information on Prairie Day along with the prairie article. In addition, we sent special letters of invitation to all known persons within about a 25 mile radius of the event who either farmed or owned prairie. We sent 150 of these letters in 1983 and 130 in 1984. We identified the prairie owners by using aerial photos to locate native prairie, then consulting farm ownership records of the county Agricultural Stabilization and Conservation Service (ASCS) offices.

SURVEY TECHNIQUES

To learn about Prairie Day participants and to help evaluate our success, we asked visitors to fill out program evaluation cards. The cards were distributed and collected at the prairie as people completed the activities. We only accepted cards from older children and adults. We feel that we obtained cards for virtually all of the population we wanted to survey. Selected data from evaluation of these two Prairie Days are presented here. Responses for both events generally followed similar trends. The data have been combined for this paper.

RESULTS

Participant Profile

(Based on combined data from 1983 and 1984, N = 327, but varies between categories because some respondents did not answer all questions - See Table 1.) About half (55 percent) of the respondents came to Prairie Days in groups of two to four people, and 80 percent came in groups of two to nine. A plurality of respondents came in family groups (40 percent), but groups of friends (14 percent), family and friends (18 percent), and organizations (23 percent) were also common. Of the organization attendance, the largest category was Scout groups (38 percent) followed by 4-H Clubs (21 percent). Fourteen percent of respondents resided in the county in which the Prairie Day was held, and another 50 percent resided in adjacent counties. Forty percent of respondents farmed or owned agricultural land in Missouri, and 20 percent of these had native prairie on their property.

Prairie Day was the first visit to a native prairie for about half of the respondents (53 percent). Forty-five percent of those who had previously visited a prairie had done so at a previous Prairie Day event.

About half the respondents (55 percent) felt they had at least "some" knowledge of prairie plants, animals and history before attending Prairie Day, and 16 percent thought they knew "quite a bit." A slightly higher percentage of farmers, agricultural owners, and native prairie owners felt they had more prior knowledge of prairies than respondents in other categories.

The two most important reasons given for attending Prairie Days were to see prairie wildflowers (71 percent) and to see prairie wildlife (60 percent). Twenty-three percent came because they were "just curious." Many of the write-in reasons in the "other" category involved learning about prairie and native grasses and comparing a public prairie with the respondents' own prairie land.

About half of the respondents (49 percent) learned about the Prairie Day events from the *Missouri Conservationist*, which had a statewide circulation of about 300,000 and a probable readership of over one million people. Respondents also learned of the events from friends and relatives (27 percent), newspapers (23 percent), and club announcements (23 percent). Our direct mailing to local landowners was responsible for informing 8 percent of the respondents about the event.

EFFECTIVENESS OF THE PRAIRIE DAY PROGRAM

Several questions on our evaluation card concerned the amount of knowledge and enjoyment gained at Prairie Days. Of the respondents who felt they had only "some" or "very little" knowledge of prairies prior to Prairie Days, 82 percent thought they had learned "quite a bit" from the experience. Only about half (48 percent) of the respondents who already knew "quite a bit" before Prairie Days felt they had learned "quite a bit" more about prairies. The other half of this group gained "some" additional knowledge. Interestingly, the amount learned by farm owners and those who did not own farms was almost identical (21 percent of both groups learned "some" and about 78 percent learned "quite a bit"). The important point here is that about three-fourths of all respondents in all categories thought they learned "quite a bit" from Prairie Days.

Respondents indicated high enjoyment for Prairie Days. No one indicated that the event was "not enjoyable," and only 4 percent found it only "slightly enjoyable." Ninety-six percent considered Prairie Days to be either "very enjoyable" (59 percent) or one of their "most enjoyable" outdoor experiences (37 percent). Respondents who owned land found Prairie Days slightly less enjoyable than those who did not, and prairie owners enjoyed the event slightly less than landowners who did not own prairies.

Nearly half of the respondents made additional comments on the survey forms and many took the time to write letters to the Department about the event. Comments were generally expressions of appreciation or enjoyment, and included compliments on the guides and exhibits and comments on the educational value of the event. Most of the negative comments called for better directions to the Prairie Days site and better publicity.

DISCUSSION

According to the evaluation cards, participants did enjoy themselves, and they did feel that they learned from the event. We hope landowners who attended will have significant influence on local attitudes, and possibly in land use in this prairie region. (An addition to one public prairie resulted from the attendance

of a neighboring landowner who had previously been unwilling to sell his prairie.) We are also hopeful of a "ripple effect" as their appreciation for prairies spreads to friends and relatives in their neighborhoods.

A similar ripple effect might result from attendance of youth groups such as scouts and 4-H, many of whose members come from farms and rural communities.

One of the most important spin-offs of Prairie Day has been the positive media exposure. We have received excellent coverage from local as well as major city newspapers. Prairie Days are generally well-covered by local television stations. Although media message has less impact than personal experience, Prairie Day coverage does put a message about Missouri's prairie heritage before thousands of people.

Prairie Day was begun to generate support from all Missourians for prairie preservation. However, a commitment to prairie preservation is especially important among the private prairie owners who have the immediate power to preserve or destroy native prairie. By targeting Prairie Day for both the general public and local landowners, we hope to favorably influence the attitudes of both of these important groups.

ACKNOWLEDGEMENTS

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Part 8. PRAIRIE RESTORATION

ONE DECADE OF RESEARCH IN PRAIRIE RESTORATION AT THE FERMI NATIONAL ACCELERATOR LABORATORY (FERMILAB) BATAVIA, ILLINOIS

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Abstract. During autumn of 1974, 181.2 kg (400 lb) of mixed prairie seeds were hand-collected from remnant prairies within 80.5 km (50 mi) of Fermilab and stratified at 5° C in a cooler during winter. In the first week of June 1975 these seeds were planted in 3.9 ha (9.6 a) of previously plowed and disked black agricultural soil within the accelerator ring (263 ha; 650 a) using a Nisbet drill. During the past ten years there have been twelve separate plantings (both spring and autumn), bringing the total area planted within the ring to 156 ha (385 a). Two additional plantings in 1984-1985 outside the ring added another 22.3 ha (5 5 a).

After experimenting with various types of agricultural equipment (Nesbit drill, hydromulcher, pull combine) these were abandoned in favor of equipment that was quicker and more efficient. Currently, using a front-mounted combine approximately 2265 to 4530 kg (5000-10,000 lb) of uncleaned mixed prairie seed are harvested in autumn, stored in an unheated barn during winter. In late June the seed is then sown in approximately 30 ha (75 a) of prepared land at the rate of about 4.3 kg/ha (40 lb/a) using an all-terrain spreader. Following this a cultipacker is used to compress the soil.

Restoration is now being accomplished by building a "prairie matrix" of late flowering grasses (*Andropogon, Sorghastrum, Spartina*) together with aggressive prairie forbs (*Coreopsis, Desmodium, Ratibida, Silphium*). This matrix can compete successfully with most weedy species, e.g., *Agropyron, Phalaris, Solidago*, producing a prairie sward that can be burned two or three years after initial planting. The planting area is then hand-sown with a "second wave" of prairie forbs and grasses, e.g., *Pedicularis, Petalostemum, Phlox, Sporobolus*, that do well once the weedy vegetation has been eliminated or greatly reduced. As the prairie improves, rarer species, such as, *Gentiana, Lilium* and *Habenaria*, will be introduced as seedlings to produce a community representative of the black soil Illinois prairie of pre-settlement times.

To date approximately 177.8 ha (440 a) have been planted both inside and outside of the accelerator ring, and eighty prairie and marsh species are now growing and reproducing on this restored prairie. The dominant grasses are *Andropogon gerardii* and *Sorghastrum nutans*, but other characteristic prairie grasses, such as, *Andropogon scoparius, Panicum virgatum, Spartina pectinata* and *Sporobolus heterolepis*, are increasing. With the exception of scattered patches of *Melilotus alba* and some clumps of *Solidago altissima*, the older plantings are relatively free of weedy vegetation.

INTRODUCTION

In pre-settlement times the northern two-thirds of Illinois - the Prairie State - was mainly covered with prairie, marsh and savanna. Using original surveys and the distribution of prairie soils, it is estimated that approximately 70% of the 145,000 square kilometers (56,000 square miles) or 103,000 sq km (40,000 sq mi) was prairie. Today no more than 13 sq km (5 sq mi) still exist along railroad rights-of-way, in pioneer cemeteries and on a few isolated tracts which have escaped the plow. Many of these remnants, especially the larger ones, are on poorer agricultural soils and do not represent the deep silt loam prairies that characterized most of the Illinois country.

With this in mind, prairie ecologists approached the administration of the Fermi Accelerator Laboratory (Fermilab) at Batavia, Illinois in August of 1972 about the feasibility of restoring an Illinois black silt-loam prairie on a portion of the laboratory's 2745 hectares (6800 a). After a number of discussions involving a series of proposals over a period of a year and a half, it was agreed that a prairie restoration project could be undertaken on land within the accelerator ring.

THE SITE

The ring is 2 km (1.2 mi) in diameter, 6.4 km (3.9 mi) in circumference and contains 314.2 ha (776.3 a). However, not all of the land is cultivable. A blacktop service road and a 15.2 meter (50 ft) moat containing water for cooling the ring magnets are adjacent to the inner side of the accelerator ring. In addition, inside the ring there is a large artificial lake used to replenish the water in the moat, a scattering of marshes and an open bur oak forest. Thus, the area available for prairie restoration is reduced to approximately 184 ha (455 a).

The land is almost flat, having a mean elevation of approximately 806.6 m (740 ft) with a variation of no more than 5.5 m (6 ft). It has been cultivated for more than a century and was mostly tiled. With the construction of the accelerator ring, many field tile lines were broken causing land to revert to the poor drainage characteristic of much of the pre-settlement Illinois prairies.

The ring soils were developed on a glacial outwash plain. Although seven soil types have been recognized in the most recent soil survey of the area (Mapes 1979), only three are widely found within the ring - Barrington and Mundelein silt loams and Drummer silty clay loam. The first two are deep, somewhat poorly drained, soils of uplands, having a silty loam surface layer and a silty clay loam subsoil. They developed in deposits of less than one meter (40 in) of silty material over calcareous silty or loam outwash. The Drummer silty clay loam is similar, having a deep, poorly drained, moderately permeable soil formed from silty clay outwash. The Barrington and Mundelein silt loams were associated with mesic prairie, while the Drummer silty clay loam formed under low prairie and marsh.

The original survey of the area was carried out in 1844 and showed the area covered with prairie. The surveyor's notes state "All rich, 1st rate prairie" and "Land, All rich and fit for cultivation." The extreme western portion of the ring is marked "timber" or "scattering timber" with the notes recording witness trees of white, red and bur oak "ten inches" in diameter. The area marked "scattering timber" has a transitional Wauconda silty loam with a gray A-layer. This would indicate that parts of the extreme western section of the ring were originally covered with savanna or prairie scrub. Such areas were often designated as "barrens" in the early 19th Century.

THE RING VEGETATION

Almost all of the original prairie within the ring was destroyed during the years of cultivation. Only along old fence rows and

in some of the ditches of abandoned country roads did a few prairie species survive, such as:

Andropogon gerardii (big bluestem grass)
Asclepias sullivantii (prairie milkweed)
Calamagrostis canadensis (blue-joint grass)
Lilium michiganese (Turk's cap lily)
Silphium terebinthinaceum (prairie dock)
Spartina pectinata (prairie cord grass)
Veronicastrum virginicum (Culver's root)

In the poorly drained areas, a few prairie marsh species were still found, such as:

Asclepias incarnata (swamp milkweed)
Carex hystricina (bottle brush sedge)
Carex lanuginosa (woolly sedge)
Lycopus americana (water horehound)
Lythrum alatum (winged loosestrife)
Lysimachia terrestris (swamp candles)
Mimulus ringens (monkey flower)
Senecio pauperculus balsamitae (ragwort)
Vernonia fasciculata (ironweed)

The land that would eventually be enclosed within the ring was retired from cultivation in 1970. Following a century of plowing and cultivation, the land lay fallow and secondary succession set in. After two or three years of an annual-biennial weed stage, an old-field community dominated by Eurasian perennial grasses and a few native perennial forbs established itself. Species present included:

Agropyron repens (quack grass)
Aster simplex (panicled aster)
Asclepias syriaca (common milkweed)
Bromous inermis (Hungarian brome grass)
Phalaris arundinacea (reed canary grass)
Poa pratensis (Kentucky blue grass)
Solidago altissima (tall goldenrod)

Since 1970 this ruderal old field community has maintained itself except that in certain areas a number of wood shrubs have invaded, especially along old fence rows. They are:

Acer negundo (box elder)
Cornus racemosa (gray dogwood)
Rhus glabra (smooth sumac)
Rosa multiflora (multiflora rose)
Rubus occidentalis (black raspberry)
Salix interior (sandbar willow)

In areas where there has been more severe disturbance of the soil, such as along the periphery of the moat, cottonwood trees (*Populus deltoides*) have formed small groves.

METHOD OF SEEDING

In the autumn of 1974, nearly a hundred volunteers collected seed from more than 70 species of prairie plants growing on remnant prairies within a 80.5 km (50 mi) radius of Fermilab. In February 1975 these seeds were cleaned using various sized screens. The resultant 181.2 kg (400 lb) of cleaned seed were then mixed with vermiculite in large plastic bags, moistened and stored in a cooler at 5° C for over four months. These cold-treated seeds were then taken from the cooler, spread out on a wooden floor and dried to remove excess moisture. They were planted during the first week of June 1975 using a Nisbet drill on previously prepared land. This land had been previously prepared for planting during the summer of 1974 when 3.9 ha (9.6 a) within the ring were plowed and disked. Two addition diskings were done in the spring of 1975.

Since that first seeding, there have been substantial modifications of planting techniques. The use of the Nisbet drill was discontinued after the first four sowings. This was partly because it planted in rows which are still visible a decade after planting, and partly because it was inefficient and time consuming especially when relatively large areas were planted (Table 1). It also required well-cleaned and thoroughly dried seeds to prevent clogging in the drill. A hydromulcher, using a slurry of seeds in water to spray onto the prepared soil, also proved unsatisfactory. This was because its excessive weight compacted the soil and also caused it to bog down in moist soil. During the past few years seeding has been done using a salt-spreader truck which scatters the mostly uncleaned seed onto the prepared soil. A further improvement, which is currently being used, has been the use of an all-terrain spreader with large balloon tires which distribute the weight of the vehicle more evenly, thus preventing soil compaction. It has a wider spreading arc than the salt-spreader and has a greater maneuverability over plowed and disked surfaces. A light harrow was used after sowing in the early plantings, but this was discontinued when no noticeable benefit was observed. Currently, a cultipacker is used before and after seeding to ensure good seed-to-soil contact. Mowing was done after some of the early plantings for weed control, but the practice has been generally discontinued because it frequently encourages the growth of heavier foliage closer to the ground. This in turn produces more intense shading which is deleterious to prairie seedlings.

Several plantings were done in autumn to increase the ease and efficiency of the restoration process (Table 1). However, this practice was discontinued because these autumnal plots had more islets of old field and weed vegetation than did those plots seeded in spring and early summer. Evidently disking the plots before late spring seeding inhibits weedy growth and encourages better survival of prairie seedlings.

Currently, from 2265 kg (5000 lb) to 4530 kg (10,000 lb) of seed are harvested from earlier plantings in autumn using a front-

TABLE 1. Fermi Prairie plot histories.

Plot	Date	Hectares	Acres	Method of Seeding
1	Spring '75	3.89	9.6	Nisbet Drill
2	Spring '76	4.17	10.3	Nisbet Drill
3	Spring '77	13.00	32.0	Nisbet Drill
4	Autumn '77	6.68	16.5	Nisbet Drill
5	Autumn '78	4.62	11.4	Saltspreader
6	Autumn '79	23.45	57.9	Hydroseeder
7	Spring '81	7.13	17.6	Hand
8	Autumn '81	17.58	43.4	Saltspreader
9	Autumn '82	22.52	55.6	Saltspreader
10	Spring '83	24.70	61.0	Saltspreader
11	Spring '84	16.20	40.0	All-Terrain Spreader
12	Spring '84	12.15	30.0	All-Terrain Spreader
TOTAL		156.09	385.3	

TABLE 2. Rate of seeding at Fermilab Prairie.

Plot	Seed (kg)	Hectares	Rate (kg/ha)	Seed (1b)	Acres	Rate (1b/a)
1	*181.2	3.9	46.6	*400	9.6	41.7
2	*108.7	4.2	27.1	*240	10.3	23.3
3	*203.8	13.0	15.7	*450	32.0	14.1
4	*154.1	6.7	23.1	*350	16.5	20.6
5	407.7	4.6	88.3	900	11.4	78.9
6	1359.0	23.5	57.9	3000	57.9	51.8
7	67.9	7.1	95.3	150	17.6	8.5
8	2718.0	17.6	154.6	6000	43.4	138.3
9	1259.3	22.5	55.9	2780	55.6	50.0
10	1359.0	24.7	55.0	3000	61.0	49.2
11	724.8	16.2	44.7	1600	40.0	40.0
12	543.6	12.2	44.8	1200	30.0	40.0
TOTAL	9087.1	156.2		20070	385.3	
AVERAGE			58.2			52.1

*cleaned seed

mounted combine (Table 2). This uncleaned seed, containing approximately one-third chaff, is spread onto a wooden floor of an unheated barn for drying and storage overwinter. To this harvested unclean seed there is mixed from 45 to 90 kg (100-200 lb) of partially cleaned seed, i.e., seed heads broken up and seeds stripped from corymbs and panicles. This partially cleaned seed is regularly collected elsewhere by volunteers. This is done (1) to increase the genetic diversity of the seed mix, (2) to augument those species having low populations on the restored prairie and (3) to introduce new species into the prairie.

The current planting regime is as follows:

1. In late summer an area to be seeded the following year has the vegetation mowed down to thirty centimeters or less and the soil plowed to a depth of at least twenty centimeters. Thus the alternate winter freezing and thawing kills some of the exposed weed roots and also weather levels the ground somewhat making further cultivation easier.
2. Toward the end of May, or as soon as it is possible to get into the field, the land is disked to smooth out the plow lines.
3. This is followed by a spring tooth harrowing to level the area and dislodge existing roots in the soil.
4. The soil is then cultipacked to provide a firm seed base.
5. Finally, the seed mix is then broadcast onto the prepared soil using an all-terrain spreader. After this the soil is again cultipacked to ensure good seed-to-soil contact.

SUCCESSIONAL CHANGES

Within a week after planting of the prairie seed, the seeds of annual weeds, which may have lain in the soil for years, germinate and initially dominate the tract. Among these are:

Amaranthus powellii (tall amaranth)
Amaranthus retroflexus (rough amaranth)
Ambrosia artemisiifolia elatior (common ragweed)
Ambrosia trifida (giant ragweed)
Chenopodium album (lamb's quarters)
Panicum capillare (old witch grass)
Setaria glauca (yellow foxtail grass)

Beneath these annual plants are rosettes of biennial weeds and seedlings of weedy perennials. Scattered through the planting in the shade of the dominant annual weeds are small depauperate seedlings of big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*) and a few seedlings of some prairie forbs, including yellow cone flower (*Ratibida pinnata*), prairie dock (*Silphium terebinthinaceum*) and showy tick trefoil (*Desmodium canadense*).

In the second year flowering biennial weeds dominate the plot. In addition, some annual and perennial weed species occur scattered throughout the tract. The biennial and perennial weed species which appear during this second year include:

Brassica kaber pinnatifida (charlock)
Cirsium arvense (field thistle)
Cirsium vulgare (bull thistle)
Daucus carota (Queen Anne's lace)
Erigeron annus (annual fleabane)
Melilotus alba (white sweet clover)
Rumex crispus (curly dock)
Trifolium pratense (red clover)

During the second year the prairie grasses grow more vigorously and form small clumps. Some even produce short flowering culms and set seed. Notwithstanding the dominance of the weeds, below them clumps of prairie grass are manifestly evident throughout. In the late summer this lower sward of prairie grasses produces the russet hue so characteristic of the prairie. After the third year of growth this now relatively dense prairie carpet will support a fire. Typically, this burning is done in the spring of the fourth year.

Following the burning of this third year growth, the prairie grasses during the fourth year reach heights (2-2.5 m) that are to be found in native prairies. Indian grass (*S. nutans*) is dominant during the fourth year, but during subsequent years dominance changes to big bluestem (*A. gerardii*). Prairie forbs also become more conspicuous during this year. Drought and other unpredictable events can occasionally lengthen this succession by a year or two.

THE CONCEPT OF THE PRAIRIE MATRIX

Continuous observation of the emerging prairie on the seeded plots over the past decade has shown that relatively few prairie species are able to survive the intense competition of weedy vegetation. Even though large amounts of seed are used, many prairie species do not survive when sown directly onto plowed and disked soil. If they do, they almost always appear as isolated specimens scattered throughout the tract. On the other hand, there are some species that consistently survive this weedy competition. This is true regardless of the method and time of seeding, the occurrence of drought and other vagaries of nature. Thus, it appears that the prairie is able to establish itself in stages. The more aggressive species with wider ecological tolerances enter first and prepare the way for the other species with narrower tolerances. This first stage of aggressive prairie plants has been termed "prairie matrix" in this paper. It is seed from this matrix, collected from

TABLE 3. Plant species of Fermi Prairie.

1. Agrostis hyemalis (tickle grass)
2. Alisma subcordatum (water plantain)
3. Allium cernuum (nodding wild onion)
4. Andropogon gerardii (big bluestem grass)
5. Andropogon scoparius (little bluestem grass)
6. Apocynum sibiricum (Indian hemp)
7. Asclepias incarnata (swamp milkweed)
8. Asclepias sullivantii (prairie milkweed)
9. Asclepias verticillata (whorled milkweed)
10. Aster laevis (smooth blue aster)
11. Aster novae-angliae (New England aster)
12. Aster simplex (panicled aster)
13. Baptisia leucantha (white wild indigo)
14. Bidens coronata (swamp marigold)
15. Bromus kalmii (prairie brome grass)
16. Calamagrostis canadensis (blue-joint grass)
17. Carex-annectans xanthocarpa (sedge)
18. Carex bicknellii (prairie sedge)
19. Carex cristatella (sedge)
20. Carex hystricina (bottlebrush sedge)
21. Carex lanuginosa (woolly sedge)
22. Carex lupuliformis (sedge)
23. Carex scoparia (sedge)
24. Carex stipata (sedge)
25. Carex tribuloides (sedge)
26. Carex vulpinoides (fox sedge)
27. Coreopsis palmata (prairie coreopsis)
28. Coreopsis tripteris (tall coreopsis)
29. Desmodium canadense (showy tick-trefoil)
30. Dodecatheon meadia (shooting stars)
31. Echinacea pallida (purple coneflower)
32. Eleocharis compressa (flat-stemmed spike rush)
33. Eleocharis smallii (spike rush)
34. Elymus canadensis (Canada wild rye)
35. Epilobium coloratum (cinnamon willow herb)
36. Equisetum hyemale (scouring rush)
37. Erigeron philadelphicus (marsh fleabane)
38. Erigeron strigosus (daisy fleabane)
39. Eryngium yuccifolium (rattlesnake master)
40. Eupatorium maculatum (spotted Joe Pye weed)
41. Fragaria virginiana (wild strawberry)
42. Galium boreale (Northern bedstraw)
43. Galium obtusum (wild madder)
44. Geum laciniatum trichocarpum (rough avens)
45. Glyceria striata (fowl meadow grass)
46. Gratiola neglecta (clammy hedge hyssop)
47. Helianthus grosseserratus (tall sunflower)
48. Helianthus mollis (downy sunflower)
49. Heliopsis helianthoides (false sunflower)
50. Juncus dudleyi (Dudley's rush)
51. Juncus torreyi (Torrey's rush)
52. Leersia oryzoides (rice cut grass)
53. Lemna minor (small duckweed)
54. Lespedeza capitata (prairie bush clover)
55. Liatris aspera (blazing star)
56. Liatris spicata (marsh blazing star)
57. Lilium michiganense (Turk's cap lily)
58. Lithospermum canescens (hoary puccoon)
59. Lobelia siphilitica (great blue lobelia)
60. Lobelia spicata (pale-spiked lobelia)
61. Lycopus americanus (water horehound)
62. Lysimachia ciliata (fringed loosestrife)
63. Lysimachia terrestris (swamp candles)
64. Lythrum alatum (winged loosestrife)
65. Mentha arvensis villosa (wild mint)
66. Mimulus ringens (monkey flower)
67. Monarda fistulosa (wild bergamot)
68. Panicum virgatum (switch grass)
69. Parthenium integrifolium (wild quinine)
70. Pedicularis canadensis (prairie betony)
71. Penthorum sedoides (ditch stonecrop)
72. Petalostemum candidum (white prairie clover)
73. Petalostemum purpureum (purple prairie clover)
74. Physostegia virginiana (false dragonhead)
75. Polygonum amphibium atipulaceum (water knotweed)
76. Polygonum coccineum (water heartsease)
77. Potentilla arguta (prairie cinquefoil)
78. Pycnanthemum virginianum (common mountain mint)
79. Ratibida pinnata (yellow coneflower)
80. Rorippa islandica fernaldiana (marsh cress)
81. Rosa carolina (wild rose)
82. Rudbeckia hirta (black-eyed Susan)
83. Rudbeckia subtomentosa (sweet black-eyed Susan)
84. Saxifraga pensylvanica (swamp saxifrage)
85. Senecio pauperculus balsamitae (balsam ragwort)
86. Scirpus atrovirens (dark-green rush)
87. Scirpus acutus (hard-stemmed bulrush)
88. Scirpus cyperinus (wool grass)
89. Scirpus fluviatilis (river bulrush)
90. Scirpus lineatus (red bulrush)
91. Scirpus validus (great bulrush)
92. Scutellaria lateriflora (mad-dog skullcap)
93. Silphium integrifolium (rosin weed)
94. Silphium laciniatum (compass plant)
95. Silphium terebinthinaceum (prairie dock)
96. Sisyrinchium albidum (blue-eyed grass)
97. Solidago gigantea leiophylla (late goldenrod)
98. Solidago gymnospermoides (goldenrod)
99. Solidago riddellii (Riddell's goldenrod)
100. Solidago rigida (prairie goldenrod)
101. Sorghastrum nutans (Indian grass)
102. Spartina pectinata (prairie cord grass)
103. Sphenopholis intermedia (slender wedge grass)
104. Spiraea alba (meadowsweet)
105. Sporobolus heterolepis (prairie dropseed)
106. Stachys palustris homotricha (woundwort)
107. Teucrium canadense (germander)
108. Thalictrum dasycarpum (purple meadow rue)
109. Thalictrum revolutum (waxy meadow rue)
110. Tradescantia ohiensis (common spiderwort)
111. Typha latifolia (common cat-tail)
112. Verbena hastata (blue vervain)
113. Vernonia fasciculata (common ironweed)
114. Veronicastrum virginicum (Culver's root)
115. Viola papilionacea (common blue violet)
116. Zizia aurea (golden Alexanders)

plots seeded earlier along with seeds from species of the second stage, that has been used in the more recent plantings. Species characteristic of the matrix are:

Gramineae
Andropogon gerardii (big bluestem grass)
Panicum virgatum (switch grass)
Sorghastrum nutans (Indian grass)
Spartina pectinata (prairie cord grass)

Compositae
Coreopsis palmata (prairie coreopsis)
Coreopsis tripteris (tall coreopsis)
Echinacea pallida (purple coneflower)
Parthenium integrifolium (wild quinine)
Ratibida pinnata (yellow coneflower)
Silphium integrifolium (rosin weed)
Silphium laciniatum (compass plant)
Silphium terebinthinaceum (prairie doci)
Solidago gymnospermoides (grass-leaved goldenrod)
Solidago juncea (early goldenrod)
Solidago nemoralis (gray goldenrod)
Solidago riddellii (Riddell's goldenrod)
Solidago rigida (prairie goldenrod)

Leguminosae
Baptisia leucantha (white wild indigo)
Desmodium canadense (showy tick trefoil)
Desmodium illinoense (Illinois tick trefoil)
Lespedeza capitata (round-headed bush clover)

Other
Allium cernuum (nodding wild onion)
Carex bicknellii (prairie sedge)
Eryngium yuccifolium (rattlesnake master)
Monarda fistulosa (wild bergamot)

It is interesting to note that the species listed above as the first to become established in a restored prairie, are also the last to disappear when a prairie is degraded and destroyed. This is probably due to their competitive ability (Schramm 1976).

Over time species of the prairie matrix increase their dominance within the seeded tracts. None of the weedy species are capable of preventing this takeover. Certain species, such as, Hungarian brome grass (*Bromus inermis*) and reed canary grass (*Phalaris arundinacea*) are more resistant, but eventually they also succumb. It would seem that these matrix species have a competitive edge over the non-prairie ones. It is interesting to observe the aggressive growth of the matrix species year after year as they invade the surviving islets of old field and weed vegetation within the plantings. Characteristically, isolated clumps of *Sorghastrum* or *Andropogon* will invade and eventually replace established stands of *Agropyron*, *Bromus* and *Phalaris*. Throughout the developing prairie there are numerous clumps of the weedy tall goldenrod (*Solidago altissima*) which are reduced in stature and chlorotic in appearance which would seem to be the effect of heavy competition with matrix plants. Patches of field thistle (*Cirsium arvense*) and bull thistle (*C. vulgare*) disappear completely within a few years after being invaded by prairie vegetation.

Once this initial prairie matrix has gained dominance and can be burned regularly, the native plants that are less aggressive can be introduced either by seeding or by planting seedlings. Second stage plants include:

Amorpha canescens (lead plant)
Aster azureus (sky-blue aster)
Aster laevis (smooth blue aster)
Aster ericoides (heath aster)
Baptisia leucophaea (cream wild indigo)
Bromus kalmii (Kalm's brome grass)
Dodecatheon meadia (shooting stars)
Galium boreale (northern bedstraw)
Liatris aspera (button blazing star)
Liatris pycnostachya (prairie blazing star)
Liatris spicata (marsh blazing star)
Lobelia spicata (spiked lobelia)
Pedicularis canadensis (prairie betony)
Petalostemum candidum (white prairie clover)
Petalostemum purpureum (purple prairie clover)
Phlox pilosa (prairie phlox)
Phlox glaberrima interior (marsh phlox)
Physostegia virginiana (false dragonhead)
Potentilla arguta (prairie cinquefoil)
Pycnanthemum virginianum (mountain mint)
Sporobolus heterolepis (prairie dropseed grass)
Thalictrum dasycarpum (purple meadow rue)
Thalictrum revolutum (waxy meadow rue)

Some species, such as, prairie betony (*Pedicularis canadensis*), shooting stars (*Dodecatheon meadia*) and the prairie phloxes (*Phlox pilosa* and *P. glaberrima interior*) do especially well when seeded directly into the established prairie matrix. Others should be first grown in flats and then transferred as seedlings to Jiffy "rootmaster" pots for a full season of growth prior to transplanting into the matrix during May of the following year. At this time the danger of frost is over, the water table is high and the rains are dependable. Planting at other times usually brings less favorable survival.

SPECIES COMPOSITION OF THE FERMILAB PRAIRIE

From eleven years of planting annually there are now 156.2 hectares (385.2 a) of restored prairie within the accelerator ring containing 115 species of native plants (Table 3). Of these, more than two-thirds are mesic and wet prairie species. The remainder are those of marshes. With few exceptions, almost all of the prairie species (Table 4) have been introduced into the ring during these eleven years; whereas most of the marsh plants were already present on the site. In addition to these prairie and marsh species, there are still some herbaceous weeds (Table 5) and a few shrubs, such as, gray dogwood (*Cornus racemosa*) and black raspberry (*Rubus occidentalis*), scattered throughout the prairie.

The dominant species of grasses throughout the restoration areas are big bluestem (*A. gerardii*) and Indian grass (*S. nutans*). Switch grass (*Panicum virgatum*) is also widespread. Little bluestem (*Andropogon scoparius*) and prairie dropseed (*Sporobolus heterolepis*) are confined to the earliest planting (Plot 1), while prairie cord grass (*Spartina pectinata*) is found in four plots (Plots 1, 5, 6, and 11). These latter three species are actively increasing. Blue joint grass (*Calamagrostis canadensis*) is found in a few isolated clones along former fence rows in Plot 10. Only recently has an effort been made to collect seed of this species and thus to introduce it into suitable areas within the prairie.

The distribution of forbs within the prairie is sporadic. In general, the earliest plantings are not only richest in forb species, but they also have the largest populations of these species. On the other hand, the highest populations of weeds and their greatest diversity occurs in the more recent plantings (Tables 4 and 5). Most of these differences in forb distribution are attributable to the relative age of the plantings, but some are due in part to the varying amounts of forb seed collected in the various years and used for planting.

Even within a given plot there are spatially great differences in the variety and numbers of forbs. It is not unusual to have localized areas with a wide assortment of forb species with high populations of these species; whereas, other areas are devoid of forbs. This partly may be the result of differences in soil moisture when the seeds were germinating, but it may also be due to non-uniform sowing of the seed.

In general, all plots from the earliest to the most recent show increasing numbers of species and populations of these species. Each year, species not seen previously, are observed; it appears that the seeds of many species may lay dormant for years before

TABLE 4. Species composition of Fermilab Prairie.

Species	Plot 1	2	3	4	5	6	7	8	9	10	11	12
Allium cernuum	A											
Amorpha canescens						U						
Andropogon gerardii	A	A	A	A	A	C	C	C	C	C	C	C
Andropogon scoparius	C											
Anemone canadensis	R											
Apocynum sibiricum		A	C					U	U			
Asclepias incarnata		A	A			U		U	U			
Asclepias sullivantii	R	R										
Asclepias verticillata	C	C	C	C								
Aster laevis	R							R				
Aster novae-angliae		R	C	R	R			U	U			
Aster simplex		A	C	C	U	A	U	C	A	A		
Baptisia leucophaea	R											
Baptisia leucantha	C	U	U		R	C	R					
Bidens coronata			C									
Bromus kalmii	C											
Calamagrostis canadensis										R		
Carex bicknelli	C											
Coreopsis palmata	A	U	U			R		R				
Coreopsis tripteris	C	C	C	A	C	C	U	C	R	R		
Desmodium canadense	A	R	R	R	C	R	R	C		R		
Dodecatheon meadia	R	C										
Echinacea pallida	C	R	R									
Elymus canadensis	R			U					C			
Epilobium coloratum						C						
Eryngium yuccifolium	U	C	C	U	U	U		C				
Galium boreale	U											
Galium obtusum	R											
Geum laciniatum						A		C				
Helianthus grosseserratus		C	C			C		A				
Helianthus mollis		U										
Heliopsis helianthoides	R	R	R	R	R	R		R				
Hypoxis hirsuta	R											
Lespedeza capitata	C	R					R					
Liatris aspera	R											
Liatris spicata	R											
Lilium michiganense								R	R			
Lithospermum canescens	R											
Lobelia spicata		C										
Lycopus americanus		R				C		A				
Mimulus ringens		R				U						
Monarda fistulosa	R	R	U	U	C	C	R	C		R		
Oxalis violacea	R											
Panicum virgatum	U	U	U	U	U	U			R	U		
Parthenium integrifolium	C	C	U									
Pedicularis canadensis	R	R										
Penthorum sedoides		U	U			U						
Petalostemum candidum	C		R			R						
Petalostemum purpureum	C		R					R				
Phlox glaberrima interior	R					U						
Physostegia virginiana	U	R	R	C								
Polygonum amphibium						C						
Polygonum coccineum						C						
Potentilla arguta	R		R									
Pycnanthemum virginianum	R					C		C				
Ratibida pinnata	C	C	C	A	C	A	U	C	C			
Rorippa islandica						C						
Rudbeckia hirta	U									U	C	C
Rudbeckia subtomentosa	U					U		U				
Senecio pauperculus						C						
Silphium integrifolium	C	C	C	U	U	R		U				
Silphium laciniatum	A	C	A	C	U	U						
Silphium terebinthinaceum	A	C	C	A	U	R		R		R		
Sisyrinchium albidum	R					C						
Solidago gymnospermoides						R						
Solidago riddellii								C				
Solidago rigida	R	R	R	A	U			A				
Sorghastrum nutans	A	A	A	A	A	A	A				C	C
Spartina pectinata	C				A	C					U	
Sphenopholis intermedia						R				U	U	
Sporobolus heterolepis	C											
Teucrium canadense		C	C			C		C				
Thalictrum dasycarpum	U											
Thalictrum revolutum	R											
Tradescantia ohiensis	R			R	R							
Verbena hastata		U	U			C		U				
Vernonia fasciculata			U			R		U				
Veronicastrum virginicum	R			R								
Zizia aptera	R											
Zizia aurea	U											

TABLE 5. Weed composition of Fermilab Prairie.

Species	Plot 1	2	3	4	5	6	7	8	9	10	11	12
Abutilon theophrasti											A	A
Acnida altissima												U
Agropyron repens				C		C	C	C	A	C		
Amaranthus powellii												C
Amaranthus retroflexus											U	
Ambrosia artemisiifolia								A	A			
Ambrosia trifida	U	U						U				C
Asclepias syriaca		U					C		C	C	C	C
Aster pilosus		U		U	R	C	C	C	C	C	C	C
Aster sagittifolius				C	U	C				U		C
Bidens comosa											U	
Brassica kaber											U	
Chenopodium ambrosioides												C
Chenopodium album											U	
Chrysanthemum leucantnemum								R				
Cirsium arvense						R		C	U			C
Cirsium discolor				R								
Cirsium vulgare								C		A	C	C
Coronilla varia							C					
Cyperus esculentus								R			C	
Datura stramonium												U
Daucus carota				C		C	C		C		U	C
Echinochloa crusgalli											C	
Erigeron canadensis								C				
Eupatorium altissimum									U			
Eupatorium serotinum										U	U	
Euphorbia supina											R	C
Festuca elatior											U	
Hibiscus trionum											U	
Malva neglecta											U	
Melilotus alba	C	C		C	C	U	C	C	C	A		C
Oenothera biennis									C	A	U	C
Panicum capillare												C
Panicum dichotomiflorum												C
Pastinaca sativa								C				
Phalaris arundinacea			U	U				C				
Plantago major									U			
Poa pratensis	C			C	C	C		C	U			
Polygonum pensylvanicum												C
Potentilla norvegica								U		U		
Prunella vulgaris									U			
Rosa multiflorus									U			
Rubus occidentalis				U		R		C				
Rumex crispus								U	U	U	R	
Setaria glauca											U	C
Setaria viridis							C				A	C
Solanum nigrum							U		U		U	
Solidago altissima	C	C	C	C	C	C	C	C	A	A	R	
Sonchus uliginosus						U				C		C
Taraxacum officinale	U					U			U		R	C
Trifolium pratense							C			C	R	C
Trifolium repens							U					
Verbascum thapsus									U			

Legend:
A = Abundant, C = Common, U = Uncommon, R = Rare.

germination takes place; whereas, others in the plot may go undetected for years due to the lack of obvious growth or blooming. Some species, such as, wild quinine (*Parthenium integrifolium*) and shooting stars (*Dodecatheon meadia*), may take five or more years before they are first observed.

THE NEXT DECADE

During the next ten years enrichment of the Fermilab prairie will continue with the introduction of still more "second stage" plants, and, if possible, some of those of a still later "third stage." Plants of this last stage would include Mead's milkweed (*Asclepias meadii*), prairie gentian (*Gentiana puberula*) and prairie lily (*Lilium philadelphicum andinum*). One of the stumbling blocks to the introduction of these plants with narrower ecological tolerances is the lack of knowledge about their mycorrhizal requirements. Another is the possible presence of allelopathic compounds in the soil and their affect on the growth of these plants.

Additional efforts will also be made to enrich the marshes with sedges, such as, *Carex stricta*, and the dominant grasses, such as, blue-joint grass (*Calamagrostis canadensis*) and prairie cord grass (*Spartina pectinata*).

With the completion of the planting of areas available within the accelerator ring in 1985, the prairie matrix will be seeded into additional suitable tracts available outside of the ring over the next few years. This has already begun with the planting of approximately 80 ha (50 a) outside the ring in 1984 and 1985.

Following an expansion of land areas under restoration at Fermilab and subsequent species enrichment of all restoration areas, attention will be given to the re-establishment and subsequent increase in populations of prairie animal species. Some of this has already been taking place spontaneously over the past few years. Sandhill cranes and whistling swans are stopping at the marshes and lakes of Fermilab prairie on their annual migrations. There has been an increase in marsh hawks using the prairie for hunting purposes and upland sandpipers have nested on the land. The resident trumper swans recently introduced could become a nucleus for the re-establishment of this prairie bird in Illinois.

Studies are now underway on methods of introducing prairie invertebrates, including such uncommon and rare species as the prairie earthworm (*Diplocardia communis*), the dion skipper (*Atrytone dion*) and the yellow-winged grasshopper (*Arphia zanthoptera*).

Another decade of prairie restoration at Fermilab undoubtedly will yield much additional valuable information and provide many new challenges.

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PRAIRIE RESTORATIONS IN SOUTHWESTERN OHIO: VEGETATION AND SOIL CHARACTERISTICS AFTER TEN YEARS

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Abstract. Four reconstructed prairies in Butler County, Ohio were planted in 1974. Seed of two ecotypes was used and two seedbed hardnesses were employed in combination treatments. In 1980, two of the sites [Jericho and Ecology Research Center (ERC)] were compared for phytomass production and residual soil enzyme activity. The phytomass of the ERC, dominated by C4 grasses, was greater than the phytomass of Jericho, dominated by C3 grass species. Residual soil enzyme activity was greater at Jericho early in the 1980 growing season reflecting the earlier growth of the C3 species. Analysis of soil properties of all four prairies in 1984 revealed that the ERC and Wilson had soils of significantly higher bulk density, lower field capacity, and lower organic matter content, resulting in a drier habitat. This resulted in dominance of C4 grass species, significantly greater phytomass production, and greater density of C4 flowering culms than at the C3 dominated Jericho and Peffer sites.

INTRODUCTION

As interest in the tall grass prairie has increased over the past two decades, so has concern that management practices suitable for central and western portions of the true prairie may not be applicable to eastern prairies (Stuckey and Reese 1981). Furthermore, the relict prairies of the east are too small and too fragile to allow adequate experimentation to determine best management practices. Simulated or reconstructed prairies present opportunities to explore prairie species behavior in the eastern environment.

In 1974, undergraduate students at Miami University, under the supervision of the late Dr. Roger E. Wilson, established four prairie sites (0.4 ha each) in Butler County, Ohio. The sites were considered highly similar in soil (moderate to well drained Russell-Miamian-Wynn silt loams; Soil Survey of Butler County, Ohio) and climatic characteristics. The Peffer Park site, an abandoned agricultural field made into a recreation and education use area, had been mowed regularly and was in its fourth year of old-field succession in 1974. The Ecology Research Center (ERC) site had been farmed (the last crop was rye) and was in the third year of old-field succession in 1974. The Wilson site had been a timothy grass pasture and was in its fifth year of old-field succession in 1974. The Jericho site had been farmed (last crop was corn) and was in its sixth year of old-field succession in 1974. Each site was subdivided into four quadrants, to include combinations of two treatments. Two seedbed hardnesses were employed: final mean bulk density 1.19 g cm^{-3} (hard) and 0.87 g cm^{-3} (soft; Leibovitz 1974). The soft seedbed was prepared by plowing and disking, and the hard seedbed was prepared by plowing only. Seed of two ecotypes was purchased from Wilson seed farms in Polk, Nebraska (Table 1). Each site was planted uniformly with these species, keeping northern and southern ecotypes in separate quadrants, but including reed canary grass in both (Leibovitz 1974).

At the end of the first growing season, the study group reported qualitatively greater phytomass production of the hard seedbed treatments. No other information to assess the success of these plantings was collected until 1979 when phytomass production was measured on the ERC site. That prairie was burned in the spring of 1980; and in the fall of that year, phytomass production was measured on both the ERC and Jericho sites (Annala 1980). In the fall of 1983, a comprehensive burn regime was imposed on the ERC site. Subsequent comparative measures for use in this study were taken from the control (unburned) portions of this site. Peffer prairie was burned in the spring of 1981, but no quantitative measures were taken, and no further management practices have been applied. Finally, Wilson prairie was not studied or managed until 1984 when this current study began.

In 1984, the sites differed visibly. The ERC site had a well established, mixed stand of the tall grasses: big bluestem, switchgrass, and Indian grass. A considerable amount of little bluestem was also present. Tall Canada goldenrod had invaded most of the plots; and side oats grama had disappeared almost entirely. In midsummer, the quadrants of different seed sources were readily visible.

The Wilson site also showed a mixed stand of warm season grasses. Side oats grama was well established in the southwestern

TABLE 1. Commercial seed varieties used in the 1974 plantings.

	Northern	Southern
Big Bluestem (Andropogon gerardii)	Bonilla (SD 27)	Certified Kaw
Little Bluestem (Schizachyrium scoparium)	Nebraska Native	Certified Aklous
Indian Grass (Sorghastrum nutans)	Certified Holt	Cheyenne
Side Oats Grama (Bouteloua curtipendula)	Certified Butte	El Reno
Switch Grass (Panicum virgatum)	Certified Nebraska 20	Certified Blackwell
Reed Canary Grass (Phalaris arundinacea)	?	?

(north/non-compacted) quadrant; and little bluestem was uncommon. Tall Canada goldenrod occurred in thick stands on the southern half of the site (north/non-compacted and south/compacted quadrants). The site also exhibited invasion by blackberries (*Rubus* spp.) and dogwood (*Cornus* spp.).

Peffer prairie presently consisted of a heavy stand of reed canary grass with moderate amounts of tall Canada goldenrod. Thistle (*Cirsium vulgare*) was present in the northwestern (south/non-compacted) quadrant. Only one quadrant, the northeastern (south/compacted) quadrant, which included a knoll, had considerable growth of the C4 prairie grasses. All of the planted C4 species occurred there.

The Jericho site consisted almost entirely of reed canary grass. The site's homogeneity was broken only by a narrow ditch, the original plowline between quadrants, in which several C4 grass plants occurred. A sprinkling of big bluestem individuals occurred in the southern two quadrants (south/compacted and north/compacted).

The purpose of this study was to quantify the differences among sites, by comparing vegetation, residual soil enzyme activity, and moisture-related soil characteristics. Phytomass was measured on the ERC site in 1979, prior to the first burn; and was measured again in 1980 on both the ERC (post burn) and Jericho (unburned) sites (Annala 1980). Residual soil enzyme comparisons were made at the ERC and Jericho sites in 1980. In 1984 quantitative analysis of the vegetation and soil characteristics was undertaken at all four prairie reconstructions to compare the sites ten years after the time of planting. The vegetation characteristics of phytomass, height, phenology, and flowering culm density, and the soil characteristics of bulk density, field capacity, and organic matter content were studied.

MATERIALS AND METHODS

Phytomass

In October 1979, sixteen sample plots of 0.25 m^2 were harvested from the prairie of the ERC. In October of 1980, sixteen sample plots were harvested from both the ERC and Jericho prairies. Each of the samples was separated by species, dried, and weighed.

In mid-November 1984, twenty circular clip plots (0.5 m^2 each) were taken at each site, five per quadrant. Because of the small size of the control plots at ERC, only two clip plots were taken in each quadrant. All clip plot samples were sorted by species, dried at 70° C for 48 hours and weighed.

Heights

Height measurements were taken on June 25, August 15, September 15, and October 10, 1984. Six species were monitored: big bluestem, little bluestem, Indian grass, switchgrass, reed canary grass and tall Canada goldenrod. Side oats grama was not abundant enough in any of the sites to warrant monitoring, and tall Canada goldenrod had invaded every site enough to warrant its study instead. In each quadrant of each prairie, ten blade heights and ten flowering culm heights were recorded.

Phenology

Selected phenological stages of growth were recorded for the same six species on all four sites. The time of anthesis was recorded, to compare time of flowering at the different sites, and also between northern and southern seed sources. Phenology was recorded weekly from mid-July through mid-October at the ERC site, and monthly at the other sites. The monthly sample dates were August 9, September 5, and October 3. Each phenological stage was recorded when a majority of the individuals of a species in a quadrat, had reached that stage.

Flowering Culm Density

Flowering culm density was measured to assess the reproductive effort of the prairie grasses. A rectangular plot (0.1 m^2) was placed on the ground and the number of flowering culms of each of the six species was recorded. One hundred samples were taken at each site, 25 per quadrant, except at ERC where the small size of the controls necessitated that only forty samples be taken, 10 per quadrant.

Residual Soil Enzyme Activities

Three random soil samples (0-5 cm depth) were taken from the ERC and the Jericho prairies twice monthly, from May to November. The soil samples were stored in whirlpacks at 4° C following precautions outlined by Pancholy and Rice (1972). Amylase, maltase, and cellulase activities in soil were determined following the procedures of Pancholy and Rice (1973), except that glucose was determined using the PGO Glucose Determination Kit (Sigma Chemical Company, St. Louis, Missouri; Kapustka et al. 1981). Values were recorded as mg glucose x g $soil^{-1}$ h^{-1}. Dehydrogenase activity in soil was obtained from Stevenson (1959) with modifications by Casida et al. (1964). Values are reported as mg formazan x g $soil^{-1}$ x h^{-1}.

To determine potential N_2 (C_2 H_2) ase activity, three 2-cm^3 cores were collected from each site. All soil cores were collected using a 5.0 ml syringe from which the tapered needle base had been removed. Each core was immediately placed in a 16 x 150 mm test tube with 5 ml Burk's nitrogen free liquid media (Wilson

TABLE 2. Mean phytomass (g m^{-2}) by species at ERC and Jericho prairies, (np = not present, tr = < 1 g).

	ERC 1979	ERC 1980	JERICO 1980
Big bluestem	260	215	28
Little bluestem	108	105	10
Indian grass	66	148	1
Switchgrass	28	80	np
Reed canary grass	67	9	372
Tall Canada goldenrod	72	60	74
Canada bluegrass (Poa compressa)	np	tr	38
TOTAL	600	618	522
Litter and standing dead	257	tr	379

TABLE 3. Mean 1984 phytomass (g m^{-2}) for each site, with groupings according to Student Newman Keuls. Letters indicate significantly different sites within each species. Trace amounts (tr) represent < 1% of total phytomass.

	ERC	WILSON	PEFFER	JERICO	CRITICAL DIFFERENCE .05	.01
C4 spp.						
Big bluestem	64^{a}	146^{a}	34^{b}	14^{b}	72	88
Little bluestem	28^{a}	0^{b}	0^{b}	0^{b}	4	5
Indian grass	78^{a}	1^{b}	2^{b}	tr^{b}	54	67
Switchgrass	12^{ab}	32^{a}	14^{ab}	tr^{b}	30	37
C3 spp.						
Reed canary grass	4^{c}	72^{b}	254^{a}	248^{a}	76	94
Tall Canada goldenrod	22^{b}	76^{a}	22^{b}	2^{b}	39	49
Other	12	39	10	2	-	-
TOTAL phytomass	320^{ab}	366^{a}	366^{a}	266^{b}	82	100
%C4 phytomass	89^{a}	49^{b}	15^{c}	5^{c}	33	41
Litter and standing dead	634^{b}	746^{a}	304^{d}	460^{c}	122	159

and Knight 1952). N_2 fixation was estimated by the C_2H_2 – reduction assay of Balandreau and Dommergues (1973). Incubation was at 22° C for 24 hr, after which a gas sample was collected in a 3 ml vacutainer. The C_2H_2 content was determined with a Varian Series 3740 gas chromatograph equipped with a 2 mm diam x 1.8 m column containing Porapak N. The dried soil weight of each tube was determined. The values were recorded as ug N x g $soil^{-1}$ x h^{-1}.

Soils

Three soil parameters were studied: bulk density, field capacity, and organic matter content. These measures were chosen to assess soil characteristics that have influenced the prairies during their 10 year growing period, rather than characteristics that would reflect only one season's conditions. For each parameter, soil cores were collected to a depth of 15 cm.

Bulk density was measured in 1984 by collecting 20 soil cores from each site 5 per quadrant. Immediately after each core was removed, the volume of the soil was determined by filling the resulting hole with white sand pre-measured in a graduated cylinder. The soil cores were then dried to oven dry weight (110 C) for 48 hr and weighed.

Field capacity was measured by collecting 20 soil cores from each site. This time each core was carefully placed in a 75 ml plastic cylinder, preserving the soil structure as well as possible. In the laboratory, each cylinder was saturated with water for 3 min, and allowed to drain. A wet weight was recorded for each sample followed by an oven dry weight.

Soil organic matter was determined on pooled samples of 5 cores from each quadrant by the Ohio Agricultural Extension Service.

RESULTS

Total phytomass in 1980 was greater on the ERC site than at Jericho (Table 2). Total phytomass in 1984 was greatest on the Wilson site, and least on the Jericho site (Table 3). Phytomass of big bluestem was significantly greater at ERC and Wilson prairies than on Peffer and Jericho prairies. Phytomass of reed canary grass was significantly greater on Peffer and Jericho than on ERC and Wilson. Phytomass of tall Canada goldenrod was greatest on Wilson prairie. Percentage of total phytomass consisting of C4 species was broken into three significantly different groups: ERC was highest, Wilson was intermediate, and Peffer and Jericho were lowest.

In general, blade heights went from greatest to least in the following order: Wilson, Peffer, ERC, and Jericho (Table 4). Blade heights of switchgrass fall into 3 groups in descending order: Wilson, ERC and Peffer, and Jericho. Heights of the C3 species reed canary grass and tall Canada goldenrod were significantly lower on the ERC prairie.

Flowering culm heights were greatest at Peffer prairie and lowest at Jericho for big bluestem. Switchgrass was tallest at ERC and Wilson, and shortest at Peffer and Jericho. Flowering culms of reed canary grass were tallest at Wilson prairie and shortest at ERC. Flowers of tall Canada goldenrod were tallest at Peffer and shortest at ERC.

C4 species showed greatest flowering culm density at the ERC and Wilson sites (Table 5). Reed canary grass, a C3 species, showed significantly greater flowering culm densities on the Peffer and Jericho sites. Tall Canada goldenrod exhibited greatest density at the Peffer and Wilson sites.

Analyses of variance for vegetation characteristics show that for almost every vegetation parameter, for every species studied, there were significant differences by site (Table 6). Only the phytomass of switchgrass and the flowering culm height of big

TABLE 4. Mean blade and flowering culm heights by species at four prairies, 1984, (np = not present). Different letters indicate significantly different groups within a species, according to Student Newman Keuls. Reed canary grass, a cool season species was sampled on 25 June 1984. All other species were sampled on 15 August 1984. For tall Canada goldenrod, blade and flowering heights are reported as identical.

	ERC	Wilson	Peffer	Jericho
A. Blade heights				
Big bluestem	78^{bc}	92^{a}	81^{b}	73^{c}
Little bluestem	48	np	np	np
Indian grass	89^{a}	87^{a}	77^{b}	85^{a}
Switchgrass	107^{b}	118^{a}	107^{b}	97^{c}
Reed canary grass	40^{b}	71^{a}	67^{a}	73^{a}
Tall Canada goldenrod	66^{c}	99^{a}	101^{a}	78^{b}
B. Flowering culm heights				
Big bluestem	135^{ab}	149^{ab}	202^{a}	120^{b}
Little bluestem	58^{a}	np	np	np
Indian grass	111^{b}	129^{a}	np	99^{c}
Switchgrass	119^{a}	123^{a}	106^{b}	102^{b}
Reed canary grass	114^{b}	141^{a}	120^{b}	123^{b}
Tall Canada goldenrod	66^{c}	99^{a}	101^{a}	78^{b}

TABLE 5. Mean 1984 flowering culm density (per m^2) by species with groupings according to Student Newman Keuls, (np = not present). Letters indicate significant different sites, within each species.

	ERC	Wilson	Peffer	Jericho
Big bluestem	3^{a}	3^{a}	0^{b}	0^{b}
Little bluestem	1	np	np	np
Indian grass	4^{a}	2^{b}	1^{b}	0^{b}
Switchgrass	4^{a}	4^{a}	1^{ab}	0^{b}
Reed canary grass	0^{b}	2^{b}	3^{a}	3^{a}
Tall Canada goldenrod	2^{b}	8^{a}	8^{a}	1^{b}

TABLE 6. Analysis of variance for site differences in vegetation characteristics of four prairies, 1984, (nd = no data). Reed canary grass heights are based on the June 25 sample. Blade and flowering culm heights are identical for tall Canada goldenrod.

	Phytomass	Blade Height	Flowering Culm Height	Flowering Culm Density
	p>f	p>f	p>f	p>f
Big bluestem	.0001	.0001	.1837	.0003
Little bluestem	.0001	nd	nd	.0106
Indian grass	.0086	.0001	.0376	.003
Switchgrass	.1042	.0001	.0011	.0011
Reed canary grass	.0001	.0001	.0001	.0091
Tall Canada goldenrod	.0001	.0001	.0001	.0001
Total phytomass	.0250			
%C4 phytomass	.0001			
Litter and standing dead	.0001			

bluestem did not show significant differences by site. Total phytomass differed at the 0.05 level of significance. All other parameters differed at the 0.01 level of significance.

Phenological characteristics of the C4 grasses were similar among sites. All northern seed source quadrants flowered within a week of one another, as did all quadrants of southern seed source. Differences in the time of anthesis was pronounced between northern and southern ecotypes. The northern ecotype flowered fully two weeks prior to the southern ecotype. Also, the caryopses of the northern ecotype remained on the rachis two to three weeks after anthesis compared to four to five weeks in the southern ecotype.

Residual Soil Enzymes

Amylase, maltase, and cellulase activity levels in 1980 were similar for the ERC and Jericho sites (Fig. 1). Although some differences occur between sites (e.g. May 29, Fig. 1), overall there are no consistent differences. Dehydrogenase activity (Fig. 2) and N_2 (C_2 H_2) ase activity (Fig. 3). show a similar pattern to that described for the carbohydrate-degrading enzymes.

Increases in soil moisture may have increased microbial activity at some dates. For example, when soil samples were collected on July 10 the sites were relatively wet (Y_{Soil} = −0.3 MP_a), unpublished data compared to the site on July 24 (Y_{Soil} = −3.0 MP_a). Maltase, cellulase, dehydrogenase, and N_2 (C_2 H_2) ase activity (Figs. 1, 2 and 3) show decreases occurring between these dates.

Soil Properties

In general, the hard seedbed treatment (original bulk density = 1.19 g cm^{-3}) has loosened; and the soft seedbed treatment (original bulk density = 0.87 g cm^{-3}) has compacted somewhat (Table 7). Specifically, the bulk density of the ERC and Wilson sites is significantly greater than that of the Peffer and Wilson sites.

There were no significant differences in field capacity among quadrants of the same site (Table 8). Among sites, however, means differ significantly. The Jericho site has the highest field capacity, followed by Peffer, ERC, and Wilson.

Organic matter content of the soils differs significantly by site (Table 9). Peffer and Jericho prairies show significantly higher percentages of organic matter in the soil than the Wilson prairie. The ERC site shows an intermediate value.

Analyses of variance of soil characteristics (Table 10) show that bulk density differs by site at the 0.01 level of significance. Field capacities differ at the 0.01 level, and organic matter content differs at the 0.05 level.

DISCUSSION

Results for the various vegetation and soil characteristics indicate that the four prairie sites do differ in significant ways. Although they were originally assessed to be highly similar (Leibovitz 1974),

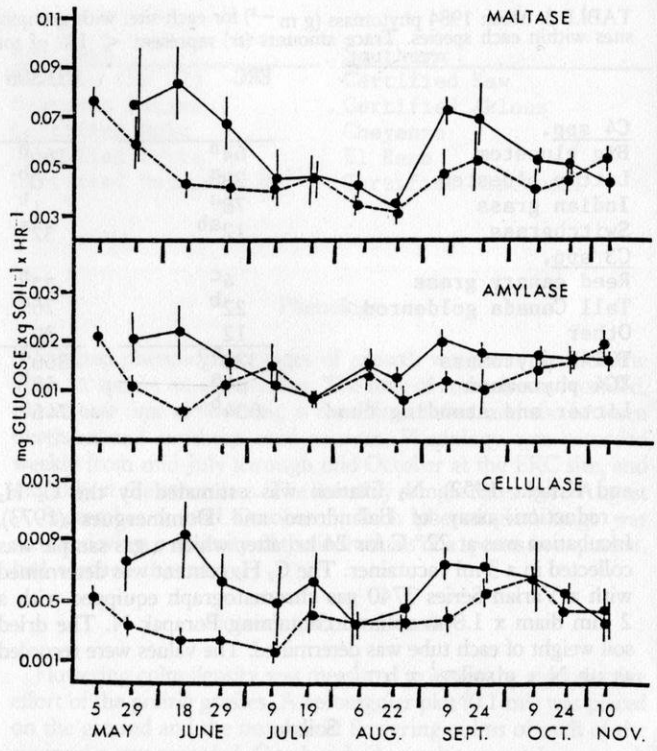

FIG. 1. Maltase, amylase, and cellulase activity levels for each site visit, 1980. Solid line denotes the Jericho site and the dashed line denotes the ERC site. Vertical lines enclose ± standard error.

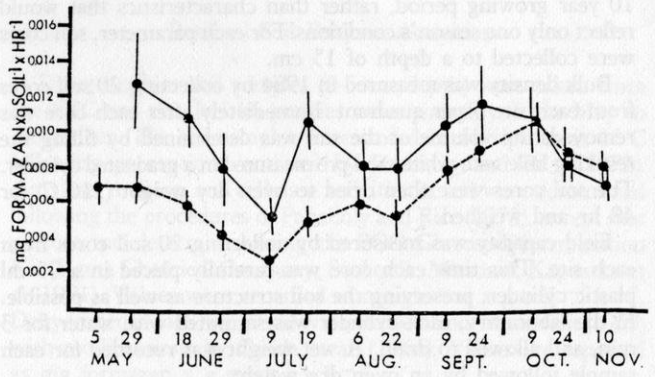

FIG. 2. Dehydrogenase activity for each site visit, 1980. Solid line denotes the Jericho site and the dashed line denotes the ERC site. Vertical lines enclose ± standard error.

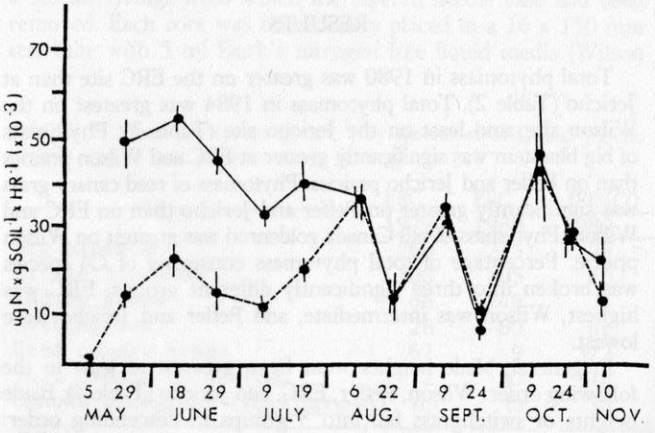

FIG. 3. One-hour assay of N_2 (C_2 H_2)ase activity for each site visit, 1980. Solid line denotes the Jericho site and the dashed line denotes the ERC site. Vertical lines enclose ± standard error.

TABLE 7. Mean 1984 bulk density (g cm^{-3}) for four prairies. Letters indicate significant differences between mean site values, according to Student Newman Keuls.

	Northern		Southern		
	Compact	Non-Comp.	Compact	Non-Comp.	Mean
ERC	.98	.95	.96	.98	.97[a]
Wilson	.94	.93	.93	.98	.94[a]
Peffer	.81	.84	.70	.81	.79[b]
Jericho	.78	.87	.84	.86	.83[b]
Critical Difference: .05 = .15					
				.01 = .18	

and were planted using identical treatments, ten years of growth have obviated site differences.

Two of the prairies, ERC and Wilson exhibit heavy stands of C4 prairie grass species, especially big bluestem. Net primary production is significantly greater on these prairies, as is sexual reproduction as measured by flowering culm density. The other two sites, Peffer and Jericho, are dominated by C3 species, primarily reed canary grass. They have lower net primary production, and lower density of flowering culms.

Residual soil enzymes are qualitative and quantitative indicators of microbial activity (Skujins 1967). Microbial activity varies in relation to substrate availability such as decomposition products and root exudates. Differences in residual soil enzymes from May to July are explainable by differences in vegetation at the Jericho and ERC sites. Jericho is dominated by early growing C3 species. During periods of growth there are increased levels of root exudates which led to improved conditions for microbes early in the growing season which resulted in elevated levels of enzyme activity. Later in the year, as C4 species began growth, abiotic conditions (mostly reduced water potentials) are not as favorable for the microbial populations.

In turn, vegetation differences appear to be related to soil characteristics. Peffer and Jericho have lower bulk density, higher field capacity, and greater percent organic matter content, indicative of more moist sites, than ERC and Wilson. ERC and Wilson prairies have greater bulk density, lower field capacity, and lower percent organic matter content.

Slight topographic variations and drainage patterns among sites may be responsible for divergence of communities over the 10 year period. Peffer prairie, which lies in a shallow basin, and Jericho, which has poor drainage as evidenced by standing water following spring thaw and heavy rains remain wet for extended periods. The ERC site is flat and only slightly better drained than the Jericho site. The Wilson prairie is on a hillside and well drained.

Prior to the May 1980 burn, the ERC prairie appeared to be shifting toward increasing dominance by reed canary grass. The effect of the fire was typical in that C4 species increased in all measures of phytomass relative to the C3 species (Annala 1981). Thus the major reason for the current vegetational differences between the ERC and Jericho appears to be the fire treatment.

In the four prairie reconstructions, phenological patterns of individual species do not appear to be influenced by soil moisture conditions. The same appears to be true of blade and flowering culm heights. Although phenology and heights do not differ dramatically by site, the paucity of tall, warm season grasses and their flowering culms at Peffer and Jericho prairies results in an impoverished appearance. ERC and Wilson prairies convey the impression of the dense stands of tall grasses characteristic of the true prairie. Peffer and Jericho prairies do not. These characteristics, along with species composition, are important to managers who reconstruct prairies for educational and aesthetic purposes, as well as botanical ones.

TABLE 8. Mean 1984 field capacity (% moisture) for four prairies. Letters indicate significant differences between mean site values, according to Student Newman Keuls.

	Northern		Southern		
	Compact	Non-Comp.	Compact	Non-Comp.	Mean
ERC	26.2	27.4	25.8	26.0	26.4[c]
Wilson	26.0	23.6	26.2	22.8	24.6[d]
Peffer	26.9	28.5	26.9	29.1	27.9[b]
Jericho	29.6	29.2	30.0	30.1	29.7[a]
Critical Difference: .05 = 2.7					
				.01 = 3.3	

TABLE 9. Mean percent soil organic matter at four prairies, 1984. Letters indicate significant differences between mean site values, according to Student Newman Keuls.

	Northern		Southern		
	Compact	Non-Comp.	Compact	Non-Comp.	Mean
ERC	2.4	3.3	2.6	2.7	2.8[ba]
Wilson	2.2	2.3	2.3	2.9	2.4[b]
Peffer	3.7	3.2	3.9	3.9	3.7[a]
Jericho	3.1	3.1	4.3	3.6	3.5[a]
Critical Difference .05 = 1.2					
				.01 = 1.4	

TABLE 10. Analysis of variance for soil characteristics of four prairies, 1984.

	Bulk Density	Field Capacity	Organic Matter
Site	.0001[b]	.0001[b]	.0392[a]
Source	.8273	.8414	.1385
Compaction	.0601[m]	.7590	.7523
Site x Source	.2293	.4134	.3871
Site x Compaction	.5054	.0001[b]	.3982
Source x Compaction	.3977	.7134	.7523
Site x Source x Compaction	.5262	.7225	--

a = significance at the .05 level.
b = significance at the .01 level.
m = marginal significance.

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PRAIRIE RESTORATION PROGRAM AT THE INTERNATIONAL CRANE FOUNDATION

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Abstract. The International Crane Foundation (ICF) is the world center for the study and preservation of endangered cranes. In 1979, ICF established an Ecosystem Restoration Program to further its goals of habitat preservation and education. The main focus of the Ecosystems program is to restore 21 hectares of the ICF site to prairie, savanna, wetland and forest. This paper will look at the 4.5 ha Federation Fields Prairie which has been planted in six different plots over a five year period. The plots have similar soil types, predominantly loamy sand, but different previous land-use, either alfalfa-brome-hay or soybeans. Seed mixes and ground preparations also varied.

Preliminary findings suggest that the best results were achieved on plots previously planted to hay, where the seeding density was 31 kg/ha or more, and where the planting occurred immediately after the last disking. Poorer results were obtained on plots previously planted to soybeans, where the seeding density was less than 30 kg/ha, and where the planting occurred several weeks after the final disking. In all, 115 prairie species were planted; 75 have appeared, and 65 have subsequently bloomed.

INTRODUCTION

The International Crane Foundation (or ICF) is located near Baraboo, Wisconsin (Fig. 1). In 1979, ICF established an Ecosystem Restoration Program to further the Foundation's goals of preserving the habitats of endangered cranes. The goals of this program are to educate the public on the importance of habitat preservation and to develop practical techniques for restoring prairie, savanna, wetland and forest communities.

In this paper we will look at the 4.5 ha Federation Fields Prairie Restoration, summarize our planting design and restoration techniques for its six different plots, and review our results to date. We hope this information will be helpful in planning small-scale restorations on similar sites.

DESCRIPTION OF THE RESTORATION SITE

The ICF property is perched on a moraine (Black 1970). The 4.5 ha restoration site lies on the ridge and the slopes of a small kettle depression. Three main types of soil underlie the restoration site: Plainfield Sand and Loamy Sand, Gotham Loamy Sand, and Wyocena Loamy Sand and Sandy Loam (Gundlach 1980). These soils are well to excessively well-drained.

According to the original Government Land Survey records of 1845, the presettlement landscape of the ICF property was oak savanna with common groundlayer species of redroot and prairie grasses (Conkey 1845, Lange 1976). Over 50 characteristic prairie and oak savanna species are still present on the ICF property (Liegel and Weber 1980).

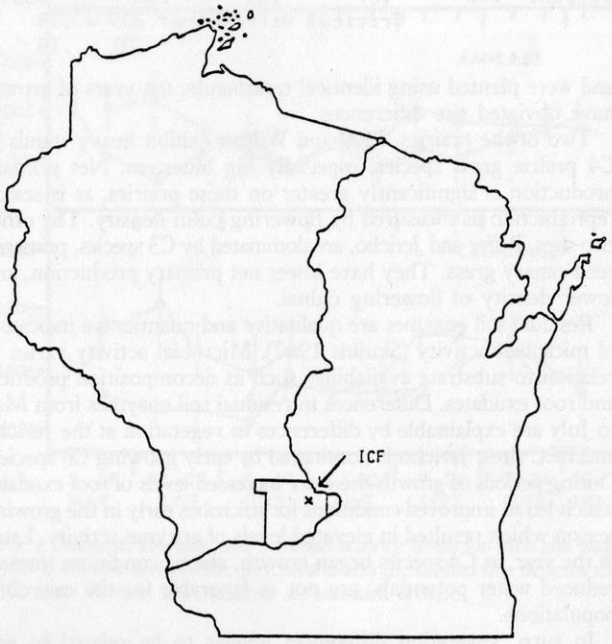

FIG. 1. Location of the International Crane Foundation (Sauk County, Wisconsin).

The restoration site was farmed soon after settlement in the mid-1850's. During the next century, farming practices generally followed a rotation of corn, soybeans, hay and pasture (Patlak 1982). At the time of restoration, the site was planted to hay, with *Agropyron repens* (quackgrass), *Bromus inermis* (bromegrass), and *Medicago sativa* (alfalfa) making up the majority of the vegetative cover.

See Table 1 for a description of the six plots of the restoration site.

PLANTING DESIGN

Previous studies have shown it virtually impossible to restore the original prairie vegetation (Blewett and Cottam 1984). However, to come as close to the composition and structure of natural prairies on similar sites, we considered the following in preparing our seed mixes: (1) the prairie types appropriate to the site, (2) the plant species appropriate to each prairie type, and (3) the relative proportion of seeds of the different species within each prairie type to be planted. See Table 2 for a description of the seed mixes used in each of the different plots.

TABLE 1. Site descriptions. International Crane Foundation's Federation Fields Prairie Restoration Project (1980-1984).

Year	Size of Planting (m^2)	Previous Use	Soil Types	Topography
1980	6300	hayfield (spring) soybeans (fall)	loamy sand	uniform
1981	9900	soybeans (1 year)	loamy sand (sand, loam)	rolling
1982A	5000	soybeans (2 years)	loamy sand (sand)	rolling
1982B	6200	hayfield	loamy sand (sandy loam)	sloping to the SW
1983	5500	hayfield	loamy sand	sloping to the N
1984	3000	hayfield	loamy sand	sloping to the SW

TABLE 2. Seed mixes. International Crane Foundation's Federation Fields Prairie Restoration Project (1980-1984).

Year	Seed Mix Types	Species # Gr-Fo-Tot	Gr/Fo Ratio	Seeding Density (kg/ha)
1980	2 (spring, fall)	12-74-86	3:2	38.1
1981	3 (dry, dry-mesic, mesic)	10-69-79	3:1	38.1
1982A	3 (sand barrens, dry, dry-mesic)	8-72-80	3:1	28.7
1982B	2 (dry, dry-mesic)	8-51-59	3:1	30.7
1983	2 (dry, dry-mesic)	8-41-49	3:2	33.2
1984	1 (dry)	9-31-40	3:2	34.0

Determining Prairie Types Appropriate to the Site

Different prairie types are generally characterized along a soil moisture gradient ranging from wet to dry (Curtis 1959). By knowing the internal drainage conditions of the different soils on the restoration site, you can match the soils with the appropriate prairie types (Anderson and Cottam 1980, Blewett 1981). We utilized the Soil Conservation Service county soil survey and field-sampling to analyze the texture and drainage conditions of the three general soils on the restoration site (Liegel and Stein 1980). We determined that sand barrens and dry prairie were appropriate to the Plainfield Sand and Loamy Sand, dry and dry-mesic prairie were appropriate to the Gotham Loamy Sand, and dry-mesic and mesic prairie were appropriate to the Wyocena Loamy Sand and Sandy Loam.

Determining Plant Species Appropriate to Each Prairie Type

To determine which species of the relevant prairie type to plant, we made lists of prairie species still found on the ICF property and on prairie remnants on similar soils within a 120 km radius of the ICF site. We chose a range of 120 km because it made seed-collecting more practical and ensured the presence of appropriate ecotypes in the restoration (Swartzmeier 1972, Wade 1981). We looked at Curtis' prevalent species lists for relevant community types (Curtis 1959) and determined the species we were able to collect or otherwise obtain in reasonable quantity. Finally, we checked our list against species range reports (found primarily in scattered volumes of the *Transactions of the Wisconsin Academy of Sciences, Arts and Letters*) and excluded any of those not reported from the near vicinity of ICF. The result of this work was a species list for each prairie type determined appropriate to the site.

Determining Relative Proportion of Seeds of the Different Species Within Each Prairie Type to be Planted

Once we determined which species were appropriate, we had to decide how much seed (by number, weight or volume) to use. We first determined our seeding rate. Because we did not have the funds or personnel to determine the viability of the seed of the different species we had collected, we generally followed the seeding rates recommended by other restorationists (Ode 1970, Rock 1974, Morrison 1981). We chose a seeding rate of approximately 1500 seeds/m^2. Depending upon the species used in the restoration and the amount of seed we had on hand, our seeding rate translated into about 29 to 38 kg/ha or 26 to 34 lbs/acre.

We then determined our grass to forb ratio. Although some restorationists have recommended ratios as low as 30:70 (Rock 1974), we experimented with 2:3 ratios, and with 3:1 and 3:2 ratios because of difficulty of collecting sufficient forb seed. These ratios are within the range of those generally considered acceptable (Smith 1980).

Finally, we determined the proportion of seeds of individual species within a seed mix by using the following method:

a. We consulted Curtis' (1959) prevalent species lists for the appropriate prairie type and used average frequency data for each species;
b. We assigned a nominal relative frequency of 1 to species not on Curtis' lists but appropriate to the prairie type;
c. We calculated relative frequencies for each species;
d. We adjusted the relative frequencies of each species to take into account growth habit, aggressiveness, difficulty of establishment, aesthetic appeal, and available seed; and
e. We determined the density by weight of each species to be added to the seed mix by multiplying its relative frequency by the grass to forb percentage of the seeding rate.

To avoid erosion of the sandy soil of the site, we added a fast-growing nurse crop, *Elymus canadensis* (Canadian wildrye), to all of the seed mixes. We initially planted at the rate of 4.5 kg/ha and later cut this to 2.25 kg/ha. Nurse crops hold the soil during the early years of the planting, and prevent invasion of exotic weed species until some of the more slow-growing native species mature (Schwartzmeier 1972, Zimmerman and Schwartzmeier 1978, Smith 1980).

RESTORATION TECHNIQUES

Restoration techniques can be categorized into three main areas: (1) site preparation, (2) seed-collection, storage and planting, and (3) short-term and long-term management. See Table 3 for a synopsis of the technique used for the six plots of our restoration site.

Site Preparation

Our restoration site was a hayfield at the time we began our restoration work. To eliminate the exotic vegetation, we used Roundup herbicide (an Isopropylamine salt of Glyphosate). We applied the herbicide at a rate of 5.2 l/ha when the vegetation

TABLE 3. Restoration techniques. International Crane Foundation's Federation Fields Prairie Restoration Project (1980-1984).

Year	Herbicide Date	Plowing, Disking Dates	Planting Date	Short-term Management
1980	May 6	May 18-21	May 24 November 22	Scything: Jl, Au 80; Ju 81 Burned: April 29, 1983
1981	May 7 spot-treated	April 15	May 9	Mowed: Au 81; Ju 82 Burned: May 9, 1984
1982A	May 24 spot-treated	May 28	May 29	Mowed: August 82 Burned: May 9, 1984
1982B	May 20	May 27-28	May 29	Pulled Sweet Clover: Ju 83
1983	May 12	May 25-26	May 28	Pulled Sweet Clover: Ju 84
1984	May 23	June 2-5	June 5	-

was 3.1 to 4.7 cm high or in its 2nd or 3rd leaf stage. Other restorationists have used Roundup to effectively eliminate exotic perennial vegetation (Woehler 1979, Nepstad 1981, Pauly 1984). Roundup is only active for a short time after application, affects only actively growing tissue, and has little, if any, residual soil affect (Weed Society of America 1983).

Following the herbicide application, we plowed and disked each plot. We limited disking to a depth of 5-8 cm to reduce the number of weed seeds brought near the surface and into a potential germination zone (Woehler 1979) and to establish a firm seed bed necessary for the prairie species to develop (Whitford 1973, Rock 1974). When possible, we disked just before planting to aid in setting back any weeds present. Smith (1980), however, has found a spring-tooth harrow to be better than a disk in bringing grass rhizomes to the soil surface where they can be killed through exposure to the sun.

After our site preparation in spring of 1980, we planted the 1981 and 1982A prairie plots to soybeans. Next year, we spot-herbicided these plots with Roundup to eliminate *Agropyron repens* (quackgrass) before planting them to prairie (Table 3). Our herbicide treatments for these plots appears not to have been effective (see RESULTS).

Seed-Collection, Storage and Planting

Members of the ICF staff, interns and volunteers hand-collected our prairie seed from remnant prairies and from a nursery established on the ICF site. We dried, cleaned and weighed the seed, and then stored it in paper bags, labelled by species, in an unheated building until the time of planting. We also scarified and inoculated the legumes with their appropriate *Rhizobium* (Burton 1972).

We seeded all of our plots by hand: six in the spring and one in late November. Our spring plantings occurred in mid-May to early June. At this time of season, weed growth is minimal (especially if seeding is done immediately after disking) and temperatures are adequate for germination of warm-season grasses and forbs (Schramm 1970, Schulenberg 1970, Whitford 1973, Smith 1980). We did not roll or harrow our planting as others have done to ensure adequate seed-soil contact (Rock 1974, Smith 1982); instead, we tried to time our planting just before a rain.

We directly seeded into a planting species which set seed in early summer, such as *Anemone patens* (pasque flower) and *Stipa spartea* (needlegrass). Our results, and those of other studies (Greene and Curtis 1950, Zimmerman 1972), have shown that these species germinate better if applied directly after seed ripens than after being stored for a while.

Management

Management techniques used at ICF include hand-scything, mowing, hand-weeding, spot-herbiciding, and prescribed burns. Periodic mowing of weeds to a 15 cm (6 in) height with a rotary mower has proved to be a successful short-term management technique for many restorationists (Rock 1974, Smith 1980, Morrison 1981). We found, however, that hand-scything of our 1980 planting was more successful than a mid-summer mowing of our 1981 and 1982A plantings, presumably because the mowing caused extensive disturbance of the site's sandy soil and because the mowing occurred just prior to an extensive period of drought.

Melilotus spp. (sweet clover) became a problem in our 1982B and 1983 plantings. We found hand-pulling the weed in mid-June before seed set very effective in eradicating it. Where hand-pulling is not feasible, other managers have found selective mowing and burning regimes helpful in controlling this weed (Heitlinger 1975, Lawrence 1981, Kline 1983, Schwartzmeier 1984).

Burning, as a management tool, has been limited because most of our plantings do not as yet have a sufficient accumulation of litter to carry a fire. Our 1980 and 1981 plots were burned in late April, 1983 and early May, 1984, respectively. Late spring burns have proved effective in controlling such cool-season exotic grasses as *Agropyron repens* (Cottam and Wilson 1966, Old 1969, Morrison 1981).

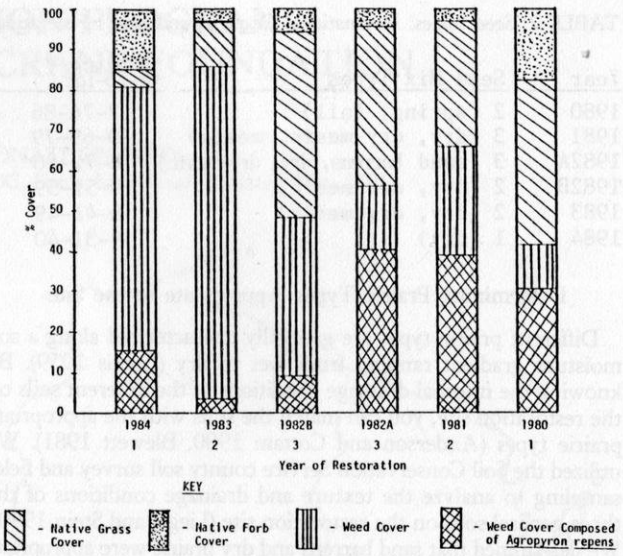

FIG. 2. Percent cover of weeds, native grasses, and native forbs. International Crane Foundation's Federation Fields Prairie Restoration Project (1980-1984).

ASSESSMENT OF VEGETATION AND RESULTS

Methods

We qualitatively and quantitatively sampled our Federation Fields Prairie plantings in the mid-summer of 1984. These data, combined with data collected on specific plots over the past five years, comprise our data base.

We sampled the individual plots by running 10 randomly placed transects across each plot. Each transect contained 25 sampling points, randomly generated, to measure aerial cover. Cover measurements were determined by using a plumb line suspended from a modified tripod. Those plant species touching the plumb line were noted as present.

We determined the percent cover per each species by dividing the number of ''presents'' by 250 (the total number of points). We grouped the cover measurements for the native grasses, native forbs and weeds to determine grass to forb to weed cover ratios.

We also noted the number of prairie species present, the number of prairie species blooming, and the general weediness of the plantings.

In addition, we determined rooted forb frequency by use of 100 0.25 m^2 quadrats. The 100 sampling points were randomly superimposed over the point-cover-matrix. Those native forbs rooted within the quadrat were noted as present.

Finally, we obtained local weather information (precipitation and temperature) for each of the past five years.

Results

The summarized results of the 1984 vegetational analysis are illustrated in Tables 4 and 5. Fig. 2 illustrates the breakdown of grass, forb and weed cover for the different plantings.

The 1984 planting consisted mostly of annual and biennial weeds. This is to be expected in the first year. The plot, however, also had an unusually high forb cover (14.5%) because of the abundance of *Rudbeckia hirta* (black-eyed susan) and *Cassia fasciculata* (patridge pea).

TABLE 4. Qualitative summary of results. International Crane Foundation's Federation Fields Prairie Restoration Project (1980-1984).

Year	Species Present	Species Blooming	Prairie Grass Establishment	Prairie Forb Establishment	Weediness
1980	69/84	61/84	excellent	excellent	somewhat weedy (20–40% by cover)
1981	40/79	35/79	good	very poor	very weedy (60–80% by cover)
1982A	34/80	25/80	good	poor	weedy (40–60% by cover)
1982B	28/59	27/59	excellent	good	very weedy mostly annual weeds
1983	18/49	9/49	good	good	very weedy mostly annual weeds
1984	12/41	7/41	good	excellent	very weedy mostly annual weeds

The 1983 plot had a minimal prairie cover - 2.5% forbs and 10% grasses. This plot is in its second year, and was dominated by *Conyza canadensis* (horseweed).

The 1982A and 1981 plantings were similar. Both had high grass covers (38% and 31%, respectively). In both, *Agropyron repens* accounted for about 40% of the cover. Presumably the site preparation, consisting of disking and spot-herbiciding, was ineffective in setting back *Agropyron repens*. In addition, the high temperatures and rainless period which followed the August mowings in 1982 and 1981 caused desiccation of forb seedlings, which may account for the poor establishment.

The 1980 spring planting fared best of all. Although *Agropyron repens* accounted for 30% of the total cover, both forb and grass cover were high, 17% and 41%, respectively. Abundant rain fell throughout the season which may account, inpart, for the success of the planting.

Our fall 1980 planting also fared well, but there were some vegetative differences between it and the 1980 spring planting. Though nearly twice as many species were planted in the spring than in the fall, more were established in the fall planting (35 versus 26). *Aster* spp. did especially well in the fall indicating that *Aster* seed should be planted immediately after collection. More weeds (75% versus 66% cover) and less prairie grasses (18% versus 25% cover), however, were found in the fall planting (Liegel and Luthin 1984). Other researchers have also noted the effect of the time of seeding on the success of directly seeded forbs (Traeger and Sutton 1983).

The 1980 spring planting was also set up to test the effects of different grass to forb ratios (3:2 and 2:3) on the subsequent composition of prairie. By the fifth year of the restoration (1984), the 2:3 seed mix had a grass to forb cover ratio of 64:36, and the 3:2 seed mix had one of 82:18 (Liegel and Lyon 1985).

Each of our plantings have been different with respect to seed mixes, grass to forb ratios, site preparation, management, and subsequent prairie cover. Nonetheless, we have noted some distinct general vegetational trends through the first five years of our restorations (Fig. 3). The first season's cover was dominated by annual weeds such as *Ambrosia artemisiifolia* (ragweed) and *Amaranthus retroflexus* (pigweed). The second season brought

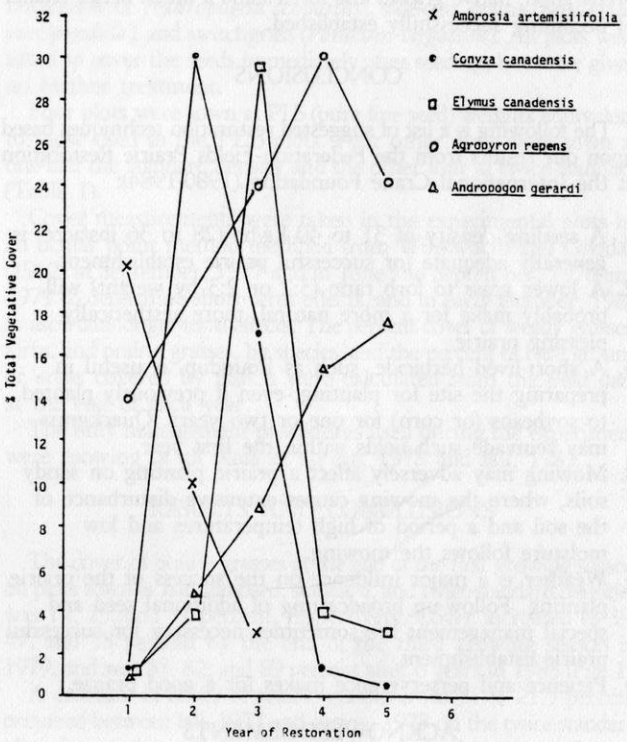

FIG. 3. Successional trends of selected weeds, native grasses, and native forbs. International Crane Foundation's Federation Fields Prairie Restoration Project (1980-1984).

TABLE 5. Quantitative summary of results. International Crane Foundation's Federation Fields Prairie Restoration Project (1980-1984).

	1980	1981	1982A	1982B	1983	1984
# Prairie Forb Species	27/76	9/69	8/72	16/51	6/41	7/33
Cover - Prairie Forbs	17%	2%	4%	5%	3%	15%
# Prairie Grass Species	6/11	5/10	7/8	5/8	5/8	5/9
Cover - Prairie Grasses	41%	31%	38%	47%	10%	4%
# Weed Species	20	9	9	15	18	24
Cover - Weeds	42%	67%	58%	48%	87%	81%
% Prairie Cover	48%	34%	43%	52%	13%	19%
% Weed Cover	42%	66%	57%	48%	87%	81%

a proliferation of the biennial *Conyza canadensis* (horseweed) as well as other weed species (especially *Berteroa incana* (hoary alyssum)). In the third season, the annual and biennial weeds showed a sharp decline, and *Elymus canadensis* (wildrye) reached its peak, becoming the dominant species. By the fourth season, *Elymus canadensis* showed a sharp decline, partly due to burning of the prairie plots after their third season, and the prairie grasses became dominant. While *Andropogon gerardi* (big bluestem) showed a steady increase in cover over time, both *Andropogon scoparius* (little bluestem) and *Sorghastrum nutans* (indian grass) maintained themselves at about the same level over the first five years of the restoration. Similar changes in vegetative cover over time have occurred on more mesic prairie restoration sites, with *Elymus canadensis* achieving dominance in the second year and prairie grasses in the third (Morrison 1981).

These yearly changes in dominance provide a tentative model for predicting the behavior of a dry prairie planting on sites similar to ICF. The model suggests that if the non-native grasses, especially *Agropyron repens*, can be suppressed effectively during site preparation, native grasses and forbs stand a much better chance of becoming successfully established.

CONCLUSIONS

The following is a list of suggested restoration techniques based upon our results from the Federation Fields Prairie Restoration at the International Crane Foundation (1980-1984):

1. A seeding density of 31 to 40 kg/ha (28 to 36 lbs/acre) is generally adequate for successful prairie establishment.
2. A lower grass to forb ratio (3:2 or 2:3 by weight) will probably make for a more natural, more aesthetically pleasing prairie.
3. A short-lived herbicide, such as Roundup, is useful in preparing the site for planting, even if previously planted to soybeans (or corn) for one or two years. Quackgrass may reinvade such fields within the first year.
4. Mowing may adversely affect a prairie planting on sandy soils, where the mowing causes extensive disturbance of the soil and a period of high temperatures and low moisture follows the mowing.
5. Weather is a major influence on the success of the prairie planting. Follow-up broadcasting of additional seed and special management are sometimes necessary for successful prairie establishment.
6. Patience and perserverance makes for a good prairie.

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THE EFFECTS OF DIFFERENT SEEDING DENSITIES ON ESTABLISHMENT OF GRASSES IN A RESTORED PRAIRIE AT PEA RIDGE NATIONAL MILITARY PARK, ARKANSAS

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Abstract. Seed mixtures of *Andropogon gerardii, Bouteloua curtipendula, Panicum virgatum, Schizachyrium scoparium*, and *Sorghastrum nutans* were sown in June, 1977 at weights equivalent to 4.33, 8.66, and 17.32 kgs per ha on replicated plots. Percent cover was determined by a point method in September, 1977 and in June and September, 1978 and 1979 to determine short-term effects of different seeding densities and in October, 1983 to ascertain longer-term effects. Cover of prairie grasses at the end of the first growing season on plots sown at low, medium, and high densities was 14, 23, and 31 percent, respectively. Cover percentages had increased to 39, 47, and 58 at the end of the third growing season and were 83, 82, and 89 percent after 6 years. This was accompanied by decreases in weedy species. Successful establishment of prairie grasses can be accomplished by the lowest seeding density used in this study, but higher densities result in more rapid establishment and fewer weed problems during the first 3 years. After 6 years, satisfactory establishment occurred at all seeding densities used in this study.

INTRODUCTION

The establishment of prairie grasses by seeding has been used in prairie restoration projects in the central United States for many years (Christiansen 1067, Landers et al. 1979 in Iowa; Schramm 1970, 1978 in Illinois; Ode 1970, Woehler and Martin 1978 in Wisconsin; Wilson 1970 in Nebraska; Bland 1970 in Michigan; Vasser et al. 1981 in Missouri; and many others).

Prairie restoration was initiated at Pea Ridge National Military Park in 1975 when the first 0.405 ha plot was established. Other plots were added each year from 1976 through 1979. Subsequent work was concerned with prairie management studies.

The methods and seeding densities used in 1975 and 1976 and results of this work have been described by Dale and Gibbons (1979). Satisfactory germination and growth of prairie grasses occurred in both plots, but it appeared that more seeds were used than was necessary during both years.

It was anticipated early in 1977 that additional restoration plots were to be added later, and that rapid development of the new restoration plots would be very desirable. It was possible also, that seed could become an important factor and quantitative information would be needed. Since procedures and results of restoration work reported from other parts of the country varied considerably and might not be applicable to Pea Ridge National Military Park, an experiment was started in 1977 to determine the short and long-term effects of different seeding densities on establishment and growth of prairie grasses.

METHODS

A site adjacent to the plots established in 1975 and 1976 was plowed and raked during the first week in June, 1977. The area was divided into twelve 0.0405 ha plots and 4 replications of 3 different seeding densities were hand broadcast in individual plots on June 15. Species used were big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), little bluestem (*Schizachrium scoparium* or *Andropogon scoparius*), side-oats grama (*Bouteloua curtipendula*), and switchgrass (*Panicum virgatum*). All plots were raked to cover the seeds immediately after seeding, but were given no further treatment.

Four plots were sown at PLS (pure live seed) weights equivalent to those used in the 1976 plots. Four other plots were sown at one-half the standard density and the other four at twice standard (Table 1).

Cover measurements were taken in the experimental plots by an ocular point method modified from Winkworth and Goodall (1962) in September, 1977 and in June and September, 1978 and 1979 to determine short-term effects, and in early October, 1983 to ascertain longer-term effects. The percent cover of weedy grasses, forbs, and prairie grasses, by species, and the percent of bare ground or areas covered by mulch were calculated from the field data at the end of each year.

The only management procedures used during the experiment were mowing of all plots in spring, 1978 and fall, 1982.

RESULTS AND CONCLUSIONS

The cover of prairie grasses at the end of the first growing season on plots sown at half-standard, standard, and twice-standard densities was 14, 23, and 31 percent, respectively. Cover increased to 39, 47, and 58 percent by the end of the third growing season in 1979, and was 83, 82, and 89 percent after 6 years in 1983 (Fig. 1).

A decrease in cover of prairie grasses from 31 to 21.5 percent occurred between fall, 1977 and spring, 1978 on the twice-standard plots. It was observed that in these plots the prairie grasses showed slow growth and incipient wilting in June. This can be attributed to the severe interference (competition or allelopathy) between the densely-planted grass seedlings. However, by fall, 1978 cover of grasses on the twice-standard plots was 38 percent, which was slightly greater than cover on the standard (32.5) or half-standard (29.0) plots.

Slight decreases in cover of prairie grasses were noted during the 1979 growing season on the half-standard and standard density

TABLE 1. Species used, ecotypes, and average PLS weights of seeds equivalent to kg per ha sown in half-standard, standard and twice-standard plots on June 15, 1977.

Species	Ecotype	Half-Standard	Standard	Twice-Standard
Big bluestem	Kaw	1.61	3.22	6.44
Indian grass	Cheyenne	.84	1.68	3.36
Little bluestem	Aldous	1.09	2.18	4.36
Side-oats grama	El Reno	.45	.90	1.80
Switchgrass	Blackwell	.34	.68	1.36
TOTAL		4.33	8.66	17.32

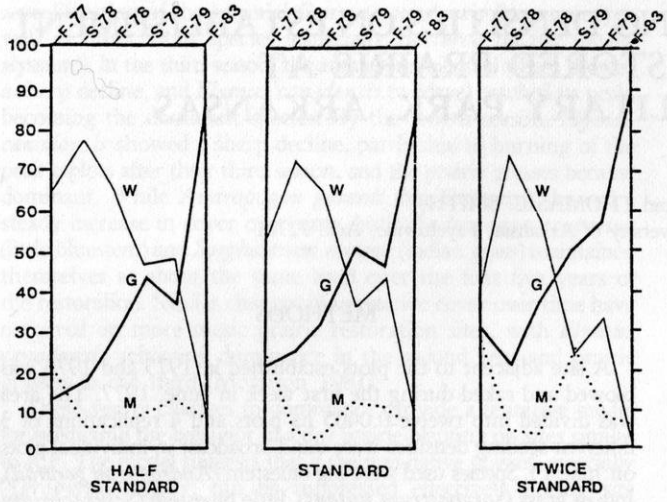

FIG. 1. Trends in percent cover of weedy grasses and forbs (W) prairie grasses (G) and percent of bare ground or mulch-covered areas (M) on plots sown at half-standard, standard, and twice-standard seeding densities. Percent cover is shown at the left and season and years of sampling at the top. F = fall, S = spring.

plots. Since slow growth and incipient wilting were not present at this time, it is possible that a combination of interference from prairie grasses, weeds, and the increased mulch cover was the likely cause.

Increases in cover of prairie grasses were accompanied by increases in weedy grasses and forbs in the half-standard and standard plots between fall, 1977 and the spring sampling period in June, 1978 (Fig. 1). This increase apparently occurred because the grass seedlings and weeds were too far apart in the thinner plantings for interference to occur until sometime during the summer. Cover of weedy species at the end of the experiment in 1983 was 9 percent of the half-standard plots, 12 percent on the standard and only 4 percent on the twice-standard. The principal weedy species present on all plots was blackberry (*Rubus* sp.) which occurred as small sprouts. Others, all of which were sparsely present on all plots were annual ragweed (*Ambrosia artemisiifolia*), purple lovegrass (*Eragrostis spectabilis*), broomsedge (*Andropogon virginicus*), and goldenrod (*Solidago* sp.).

Initially areas between prairie grasses and weedy species consisted of bare ground. Most of this bare ground was covered by mulch after fall, 1977. The bare places and areas covered by mulch considered collectively showed fairly consistent trends throughout the study except that mulch increases were much higher in 1979 on the twice-standard plots. The relatively thin mulch cover of less than 5 percent on all plots in fall, 1978 was caused by mowing in spring, 1978. Similar declines to less than 8 percent by fall, 1983 are attributed to mowing in fall, 1982 (Fig. 1).

Results of this study suggest that successful establishment of prairie grasses can be accomplished by the lowest (half-standard) density, but higher densities will result in more rapid establishment and fewer weed problems by the end of the third growing season. After six growing seasons it does not appear to make much difference which initial seeding density is used. This is in general aggreement with Schramm (1970) and Wilson (1970).

Consideration should be given to the possibility that very high seeding densities may subject the seedlings to severe interference resulting in slow growth, death of many seedlings, and poor establishment, particularly during a dry year. In contrast, it is possible that weeds may crowd out the prairie grass seedlings in the thinner plantings in years with cool, wet springs. Finally, it should be recognized that seeding densities and procedures that are satisfactory in one part of the country may not produce satisfactory results in another.

All factors considered, the standard seeding density appears to be the best for establishment of prairie grasses in the restoration plots at Pea Ridge National Military Park.

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A COMPARISON OF TRANSPLANTING TIMES AND METHODS FOR SALVAGING PRAIRIE FORBS AND GRASSES

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Abstract. Although prairie remnants are rapidly being lost to agriculture and development, salvage operations prior to their destruction may be undertaken to preserve the plants and local genotypes. This field study examines the relative success of transplanting forbs and grasses according to different methods, weather conditions, and seasons. The methods include: root-pruning individual forbs prior to transplanting; transplanting individual forbs without root-pruning; and transplanting sod manually and with earth-moving equipment. Root-pruning was done in fall of 1982 and spring of 1983 and monitoring continued until fall of 1984.

Results varied according to species. For most species there was little difference between spring, summer and fall transplantings. Root-pruning did not substantially increase survival of most forbs. Sod transplants resulted in the successful salvage of many species of native grasses and forbs, as well as several exotic species. These results indicate that most prairie species can be successfully transplanted at any time of the year if done under the proper weather conditions, which include cool temperatures, high humidity, and overcast skies.

INTRODUCTION

Once a vast expanse of the landscape, the native prairies of North America have dwindled to a few isolated remnants. Despite preservation efforts, increasing demands for housing, highways, and farmland eliminate more of these prairie remnants each year. In cases where destruction is imminent, it may be advisable to salvage the plants for use on other sites in order to mitigate the environmental effects and preserve local genotypes. However, many such opportunities have been thwarted by the belief that since prairie plants have extensive root systems, they will not survive transplanting. When salvaging attempts are made, they generally occur on short notice and without regard for time or weather conditions. These transplants have resulted in varying degrees of success, although systematic monitoring of transplants has occurred only rarely.

Recently, Weber (1982) and Svedarsky (1982) transplanted strips of prairie sod 8 cm and 5 cm thick, respectively, using commercial sod cutters. Weber found that in comparison to an adjacent seeded area, many of the prairie species in the sod transplants were initially killed, stunted, or choked out by competing weedy vegetation. Yet burning and mowing encouraged regrowth and germination of the native species. Though the prairie sods required more time and effort for planting than did the seeded plots, a greater variety of prairie species emerged from the seed bank stored in the sod. Svedarsky found that many prairie species could be transplanted even during active periods of growth. Prairie species survived and dominated sods transplanted to a gravelly, infertile site, while weedy grasses overtook sods transplanted to a fertile topsoil site.

Drake (1983) used several methods to save plants from a steep hillside prairie. Approximately one-third of the small forbs (wildflowers) and most of the grass clumps resprouted from turf rolls cut by a bulldozer. Sod slabs cut and run over by a scraper recovered much more slowly. A labor-intensive method of ball and burlap transplanting resulted in approximately half of the forbs surviving.

This study explored two new methods for recovering prairie plants: root-pruning and the use of heavy earth-moving equipment to move individual pieces of sod. Root-pruning is a technique whereby the roots of a plant are severed while the plant remains in the ground, forcing the plant to produce roots in a compact mass. It is commonly used on woody plants in horticultural nurseries to decrease transplanting shock, and generally occurs one to several years prior to transplanting (Janick 1972). The use of earth-moving equipment such as front-end loaders to move mature prairie plants has been explored very little, but could be accomplished by construction contractors, highway crews, and others to salvage plants from roadside remnants prior to grading the site. If proven feasible, both methods could be used to mitigate losses due to construction or plowing, by moving the plants to nearby roadsides, parks, or lawns.

STUDY AREAS

Highway Prairie Site

All the plants for this study were taken from a degraded remnant prairie in Marquette County, Wisconsin (T15N R9E Sec. 30 SW, 31 NW). Approximately twelve ha of sand prairie were destroyed in the fall of 1984 in preparation for the widening of U.S. Highway 51. The soil on the site was a Moundville loamy fine sand with a pH of 6.8. Although the prairie contained several exotic weed species, the abundance of prairie forbs was relatively high. Of special interest was a conspicuously large population of wild lupine (*Lupinus perennis*). Sod pieces that were transplanted mechanically were moved into an area of similar soil type and topography adjacent to the prairie. This area will be on the right-of-way of the new highway and will be protected during construction.

Oldfield Site

All manual transplants were moved from the highway prairie site to a site three km away (T15N R8E Sec. 27 NE). The site had been planted in corn through 1981 and was cultivated just prior to transplanting. The soil here is also Moundville loamy fine sand, with a pH of 6.0 and a slightly higher silt content than that of the highway site. The average slope at both sites was 0 - 3%, although the highway site did contain a small roadcut area with a slope of approximately 30%.

METHODS

I used two distinct transplanting procedures: transplanting individual forbs; and transplanting intact pieces of prairie sod.

Individual Forb Transplants

Treatments varied by time of root-pruning (fall, spring, and control (not root-pruned)) and time of transplanting (spring, summer, fall and control (not transplanted)) (Table 1). Each

TABLE 1. Treatments for individual forb transplants.

Time of Transplanting	Time of Root-pruning		
	Fall 1982	Spring 1982	Control
Spring 1983	X		X
Summer 1983	X	X	X
Fall 1983	X	X	X
Control	X	X	X

TABLE 2. Forb species characteristics. Nomenclature from Gleason and Cronquist (1963).

Species	Flowering Times	Root Structures
Anemone cylindrica Gray thimbleweed	June-August	Shallow, fibrous
Asclepias tuberosa L. butterfly-weed	June-August	Thick taproot
Aster linariifolius L. savory-leaved aster	August-October	Deep, fibrous, occasional rhizomes
Liatris aspera Michx. blazing star	August-October	Woody corm
Lithospermum caroliniense (Walt.) MacM. hoary puccoon	May-July	Thick horizontal and taproots, woody
Lupinus perennis L. wild lupine	May-June	Thick taproots and rhizomes
Monarda punctata L dotted horsemint	July-October	Shallow, fibrous
Phlox pilosa L. prairie (downy) phlox	April-June	Shallow, fibrous
Rosa carolina L. pasture rose	June-August	Thick horizontal and taproots, woody

treatment consisted of ten plants from each of nine forb species representing a wide variety of flowering times and root structures (Table 2).

To root-prune individual forbs I inserted a 25 cm deep spade into the soil 15 cm from the base of the plant, and cut at an angle on all sides of the plant such that tap roots directly below the plant were severed at an approximate depth of 15 cm. Plants remained in the ground at least 2 months prior to transplanting. When dug, the soil around the plants was cut at the same 15 cm line as the root-pruning.

Transplanting was done in late afternoon and early evening to reduce stress on the plants. This time of day is generally accompanied by low light levels, temperatures, and wind velocity, and high levels of relative humidity, thus minimizing transpiration rates, root exposure and desiccation. The plants were placed in wooden flats, transported, immediately replanted, and watered twice: once at the time of transplanting and again the following morning. This procedure was used to simulate large-scale salvage operations where little or no water may be available to the transplants.

For each plant in each treatment I recorded plant height, number of stems, flowering condition, vigor and survival on the following schedule: immediately prior to root-pruning and/or transplanting, two weeks following root-pruning and/or transplanting, and three times during the following growing season.

Manual Sod Transplants

Treatments varied by time of transplanting (spring, summer, fall and control (not transplanted)) with each treatment consisting of twenty randomly selected sod pieces 30 cm x 30 cm x 15 cm deep. They were cut and dug out with a spade, transported to the oldfield site in wooden flats, immediately replanted and watered twice: once at the time of transplanting and again the following morning. Transplanting was done in early afternoon and evening to reduce stress on the plants. Using the same monitoring schedule noted above, I recorded species presence, flowering, and vigor for all species, percent cover for all grasses and sedges, and presence of first year seedlings. Both weedy and native prairie species were monitored.

Mechanical Sod Transplants

An operator with a front-end loader (tractor with a scooping bucket) performed the entire mechanical transplanting operation on November 10, 1983. The transplant site along the nearby right-of-way was prepared by scraping off the vegetation present, leaving a flat bed of sand. Sections of sod, approximately 100 cm x 150 cm x 15 cm deep were scooped up, moved to the prepared site, and laid atop the sand. The operator placed sod pieces contiguously without breaking or flipping the sod. The sods were not rolled after planting. No watering was done on this treatment. Species presence data were taken on this treatment the following year and compared with presence data from the entire prairie remnant site prior to destruction.

RESULTS AND DISCUSSION

A preliminary analysis of the data shows that each of the forbs studied was able to survive individual transplanting with some degree of success (Table 3). Species having the greatest survival rates included those with a shallow fibrous root system (e.g., *Aster linariifolius* and *Phlox pilosa*) or species such as *Liatris aspera*, which has a small woody corm at the base of the plant and few other roots. The species having the lowest survival rates were *Lupinus perennis* and *Lithospermum caroliniense*, both of which have thick rhizomatous roots that extend both laterally and vertically for several feet. When digging these species, many of the roots were cut off and left in the soil. In the following year, new lupine and puccoon shoots emerged from the bare ground where the plants had been excavated.

Most of the species transplanted without root-pruning showed little difference between spring, summer and fall transplanting. This result may be attributed in part to the extra care taken to transplant only in the late afternoon and early evening hours. If transplanting were done in the heat of the midday sun, it is likely that a greater difference would have occurred between planting seasons. Although many people believe that transplanting can be done successfully only in the spring or fall, many of the species in this study actually performed slightly better when transplanted in the summer. I found no correlation between flowering time and optimal transplanting times for any individual species.

Root-pruning increased survival for only a few of the species and in only one of the treatments. *Lithospermum caroliniense* and *Lupinus perennis* both showed a higher survival rate when root-pruned in the fall and transplanted in the spring, when compared with unpruned transplants from any season (Table 3). These two species were also the only ones with 100% survival from root-pruning only in both fall and spring root-pruning trials. These results indicate that root-pruning may be useful for thick-rooted species that are normally very difficult to transplant. A greater length of time between root-pruning and transplanting may cause more significant results in survival rates for the various treatments.

For one species, *Monarda punctata*, root-pruning actually lowered the survival rate. Approximately 65% of all *Monarda punctata* plants that were root-pruned were dead or dying two

TABLE 3. Percent survival of forbs by species and treatment.

	METHOD OF TREATMENT											
	No Transplant Root-prune only in:		No Root-prune Transplant only in:		Root-prune in Fall Transplant in:			Root-prune in Spring Transplant in:			Total avg.per species	Control Root-prune No tsplt
	Fall	Spring	Spring	Summer	Fall	Spring	Summer	Fall	Summer	Fall		
Anemone cylindrica thimble weed	100	90	100	90	100	90	80	70	80	70	87	100
Asclepias tuberosa butterfly weed	60	70	80	80	70	80	80	70	90	50	73	90
Aster linariifolis flax-leaved aster	90	100	90	80	90	100	90	90	100	100	93	100
Liatris aspera blazing-star	100	100	90	100	90	100	100	90	100	90	96	100
Lithospermum caroliniese hoary puccoon	100	100	20	30	0	60	30	20	0	30	39	100
Lupinus perennis wild lupine	80	30	30	40	10	80	10	10	20	10	32	100
Monarda punctata dotted horse-mint	30	10	50	60	90	60	50	40	80	20	49	90
Phlox pilosa prairie phlox	100	80	70	100	90	90	90	90	70	70	85	100
Rosa carolina pasture rose	100	80	70	100	90	90	40	90	60	60	78	90
TOTAL average per treatment	84	73	66	76	70	83	63	63	66	56	-	97

weeks later. These plants were growing along the steeper roadcut with no other plants immediately surrounding them. Root-pruning caused a shallow depression around the base of the plant, exposing the shallow roots and apparently causing their death.

Many of the forbs that appeared to be dead at the time of transplanting or when observed two weeks after planting, reemerged the following year. Evidently, the top of the plant died back under stress while the roots and underground reproductive structures remained alive. The high root-to-top ratio in prairie plants encourages this mechanism of adaptation to disturbance. This common occurrence of top die-back after transplanting must be taken into account when assessing survival, by giving the plants at least a full growing season to recover.

In both mechanical and manual sod transplants most of the species of grasses and forbs survived (Table 4). 87% and 89% of the native forb species survived mechanical and manual transplanting, respectively. 100% of the native grasses survived both methods of sod transplants. 100% of the exotic grasses and forbs also survived both transplant methods. In many cases these weedy species dominated the sods for the first year. Many of the exotics were annuals and biennials that typically flourish the first year after disturbance. It is early yet to determine if native species will eventually dominate the sods, although it appears likely. More research is needed to determine whether the weedy species are harmful as competitors for light, water, and nutrients, or if they are helpful as a cover crop for the native prairie species.

In general, large grass clumps, young seedlings, and first-year forbs had the best survival rates for all the prairie species in both manual and mechanical sod transplants. In the year following transplanting, it was apparent that many seedlings had emerged since the time of transplanting, especially those of *Lupinus perennis*. The seeds were carried in the sod, forming a seed bank that would not be present in a planting using only nursery stock. Weed seeds were also transplanted with the sods, but they also occur in cultivated soils where prairie plantings are usually done. Soil disturbance often triggers germination of both weedy and native species.

Advantages of Restoration by Transplanting Mature Plants and Prairie Sod

In comparison with planting a prairie restoration or reconstruction with seed or nursery-grown stock, there are advantages and disadvantages of using mature plants or sod salvaged from a prairie remnant.

Biotic Diversity

By utilizing natural prairie plants from an area that would otherwise be destroyed, some of the biotic diversity of the original prairie can be preserved. This may be a valuable asset for saving rare species or unique genotypes, such as, yellow-flowered butterfly weed (*Asclepias tuberosa*) and pink-flowered lupine (*Lupinus perennis*) found at this site. Preserving the local genotypes may also be important when salvaging plants from the last remaining prairie in a given geographical region.

Transplanting a piece of prairie sod moves much more than just the conspicuous grasses and forbs. The sod also contains the proper soil for the plants, an established seed bank, valuable mychorrhizal fungi, insects, soil invertebrates, and rhizobia bacteria that allow the legumes to fix atmospheric nitrogen. Because large numbers of plants and seeds are stored in sod, plantings using natural prairie sod are closer to true prairie restorations than those using seeds and/or nursery stock.

TABLE 4. Numbers of surviving and invading species in prairie sod one year after transplanting.

	Manual Transplant			Mechanical Transplant		
	Present Prior to Transplant	Surviving Transplant	New Invaders	Present Prior to Transplant	Surviving Transplant	New Invaders
Forbs (native)	55	49	0	55	48	0
Forbs (exotic)	22	22	3	22	22	3
Grasses (native)	10	10	0	11	11	0
Grasses (exotic)	5	5	0	5	5	0
Sedges (native)	1	1	0	2	2	0

However, when relying on salvaged prairie plants, a project is limited to the species that exist on the original prairie and that can also withstand the rigors of transplanting. This limited diversity could later be supplemented by interspersing additional plants or seeds. Utilizing prairie sod also carries the risk of introducing unwanted species into a planting, especially when the site from which the plants are taken is degraded and weedy, as is often the case with remnants along roadsides and farm fields.

Time

Creating a prairie planting from established plants rapidly fabricates a cover with aesthetic and ecological benefits. This compares favorably with the 3 - 5 years necessary for a seeded prairie planting to fill in and cover bare patches of soil. Salvaged prairie sods have great potential use for roadbanks and other areas where immediate erosion control is required.

The planting time required when using prairie sods depends on the technique and equipment used, and on the distance between the original prairie and the planting site. If construction or farm equipment and a skilled operator are available, several hectares could be transplanted in a single day. Hand transplanting is a very slow process, whether using mature plants or nursery-grown seedlings. For this study, digging, transporting and replanting plants took approximately 3 hours for 1.8 square meters (20 square feet), not including time spent for soil preparation or watering the plants when initially planted. In situations where volunteers are available to aid in the transplanting, many more plants can be moved in a given period of time. Seeding is generally the most rapid method of reconstructing a prairie, although seeded sites may take the longest time to resemble and function as a prairie.

Costs

The cost of salvaging plants from a prairie remnant depends on the scale of the operation and the equipment and labor available for use. At a small scale, such as a truckload of plants taken for a small project, costs are minimal. These will generally include only site preparation, transportation and the time of the persons involved. However, rental of a sod-cutter, front-end loader or other equipment could be quite expensive. In many situations the plants could be salvaged with the same equipment that is being used to destroy the prairie. In these cases the additional costs of transplanting may depend only on the extra time and labor needed to move the plants before grading the site.

In general, the costs when using salvaged plants consist only of the cost of equipment and labor. In contrast, a major cost for most traditional prairie plantings is the cost of seed or plants. Table 5 shows an example of costs for seed only (no labor, soil preparation or maintenance costs are included) for 0.4 hectares (1 acre) of a typical mesic prairie planting. For these plantings equipment and labor costs may also be quite high. As the costs of restoration vary greatly for each site, no generic economic comparison can be made, although certainly in many cases the cost of using mature plants rescued from threatened remnants is substantially lower than for either seeding or using nursery stock.

TABLE 5. Estimated cost of prairie seed for 0.4 ha (1 Acre) of a Mesic Reconstruction.

Seeding Rate[1] - 20 lbs pure live seed (pls)/acre[2]
Grass to Forb Ratio[1] - 85:15 = 17 lbs pls:3 lbs pls[2]

Grass Species Composition[3]	%	lbs pls		Price per pound		Total cost
Andropogon gerardi	40%	6.7	x	$40	=	$268
Sorghastrum nutans	30%	5.1	x	20	=	102
Panicum virgatum	15%	2.6	x	75	=	195
Andropogon scoparius	15%	2.6	x	40	=	104
	100%	17.0 lbs pls				$669

15 forb Species[3] @ 1% each of total Composition = 15% or 3 lbs pls total

Species	Price[4] per lb.	x .20 lbs	= Total Cost
Amorpha canescens	$ 76		$ 15.20
Baptisia leucantha	320		64.00
Coreopsis palmata	288		57.60
Echinacea pallida	160		32.00
Eryngium yuccifolium	200		40.00
Heliopsis helianthoides	106		21.20
Lespedeza capitata	192		38.40
Liatris aspera	53		10.60
Monarda fistulosa	240		48.00
Petalostemum purpureum	53		10.60
Ratibida pinnata	92		18.40
Rudbeckia hirta	400		80.00
Silphium laciniatum	200		40.00
Solidago rigida	35		7.00
Veronicastrum virginicum	320		64.00
		Total forb seed	$ 547.00
		+	
		Total grass seed	$ 669.00
		Total cost of seed	$1,216.00/acre

[1]Morrison, Darrel. unpubl. paper. 'Notes on the Design and Establishment of Prairie Plantings'
[2]1 acre = 0.4 ha, 1 lb = 0.45 kg
[3]Burley, Jon Bryan, 1984. "Prairie Landscaping. Insuring a Prairie future: Blue Cross Blue Shield Tour."
[4]Price list from Prairie Ridge Nursery, Mt. Horeb, WI, 1985.

CONCLUSIONS

This study suggests that time of day and weather conditions at the time of transplanting may have more effect on transplant survival than does time of year. Prairie forbs and grasses may be successfully transplanted throughout the growing season, if done during cool, cloudy and humid conditions. Although root-pruning was not an important factor in increasing transplant survival rates of most species, it did enhance survival for species with long thick roots which are typically difficult to transplant, such as *Lithospermum caroliniense* and *Lupinus perennis*. Transplanting pieces of sod, either manually or mechanically, can result in a very high rate of survival for the majority of the prairie and weed species. Sod transplants also result in the transportation of seeds, dormant rootstocks, and soil organisms that may increase the overall success and diversity of the planting.

This study does not advocate the collection of prairie plants from undisturbed remnants, but considers optimum times and methods for rescuing native plants that would otherwise be destroyed. Recommendations from this study may prove useful throughout the prairie community, wherever remnants are threatened by development. Prairie enthusiasts should work with the local highway crew, farmer or developer to salvage the prairie plants and preserve at least the top layer of the prairie that once existed.

ACKNOWLEDGEMENTS

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THE ROLE OF STATE FOREST NURSERIES IN PRAIRIE PLANT PROPAGATION

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Abstract. Germination and establishment of forb species in seed mixes has proved to be of limited success. Because of the high cost of most forb seed and the fact that seeds of local genotypes are not often available commercially, a more successful, cost effective method of forb establishment is desirable.

Many prairie forbs lend themselves well to standard forest nursery techniques because of the nature of their root systems and their perennial habit. In 1980 the Illinois Department of Conservation began raising selected forb species at its Mason State Nursery to provide plants for prairie restoration projects. The Missouri Department of Conservation initiated a similar project in 1983. Seeds are hand collected from local native sources and sown into beds in the fall. After two years most species flower. Seed is collected and plants are lifted using standard nursery equipment. They are distributed bare-root and transplanted in the fall. This method appears to be successful with a number of species, including leadplant (*Amorpha canescens*), prairie clover (*Petalostemon* spp.), compass plant (*Silphium laciniatum*), blazing star (*Liatris pycnostachya*), rattlesnake master (*Eryngium yuccifolium*), and pale purple coneflower (*Echinacea pallida*).

INTRODUCTION

A variety of private and public universities, arboreta and other organizations have been involved with prairie restoration efforts over the past fifty years. Since the early 1970's state and federal conservation agencies have become increasingly involved in using and promoting the use of native prairie forbs and grasses in wildlife plantings.

The Illinois Department of Conservation became involved in prairie restoration at Goose Lake Prairie State Park in 1975. It soon expanded its efforts with the objective of developing replicates of the prairie that once covered some 8,800,000 hectares of the state during presettlement times. In 1981, the Department's Division of Fish and Wildlife Resources became interested in using native prairie grasses in a "Roadsides For Wildlife" project.

The Missouri Department of Conservation began planting native warm season grasses and forbs on its wildlife areas as early as 1968. By 1979, the program had expanded to promoting the use of native warm season among landowners for pasture and hay production. In 1984 the Department received 138 requests to plant 960 ha of native warm season grasses on state and private land.

Obtaining enough native grass and forb seeds for use in state agency programs like those in Illinois and Missouri can be a problem. The cost of forb seeds is very high, ranging from $100 to $400 a kilogram ($50 - 200/lb) and often seeds are either not available or not in the desired quantities. Secondly, and more important, large quantities of native ecotype material are often not available. In 1977, the Illinois Department of Conservation saw a need for the production of native ecotype grass seed to meet its demands, because its prairie restoration program was based on the use of native plant materials. Grass seed collection areas were established at the Department's Mason Tree Nursery in Topeka. Forb species were added in 1980. The Missouri Department of Conservation began growing forbs at its nursery in 1983. The plants are initially intended for use on Conservation Department lands. This paper will discuss the experiences of the Mason Tree Nursery in Illinois and the George O. White State Nursery in Missouri in growing native grasses and forbs for use in their Departments' restoration and planting programs.

MATERIALS AND METHODS

Illinois

The Mason Tree Nursery began prairie plant production in the fall of 1977 with a 0.68 ha plot of big bluestem (*Andropogon gerardii*) and 0.52 ha of Indian grass (*Sorghastrum nutans*). Seed for the initial planting was native ecotype material purchased from Dr. Peter Schramm of Knox College. By the fall of 1979 they combined 157 kilograms of big bluestem seed from the 0.68 ha plot. The Indian grass started very slowly and was reseeded in 1981. In 1982 the Illinois grass plantings were expanded to 3.6 ha to provide enough seed for restorations and the Roadsides for Wildlife project. The 1983 drought slowed the development of this area.

In 1980 the Illinois Department of Conservation began growing native forb species at the Mason Nursery after reviewing the forb operation of Dick Camp at the F.G. Wilson Nursery in Wisconsin. Seeds of six species were purchased from Dr. Peter Schramm. Twenty-eight grams of each species were fall planted in standard nursery seedbeds using 4.5 m^2 per species. In addition, seeds of six additional species were collected by staff biologists. These were planted in standard nursery beds in the spring of 1981. Plants were grown for two seasons with the intent of collecting seed during the second year of growth. Seed production of the initial plantings exceeded expectations, with most species producing seed the first year. The 53^2 m (576 ft^2) planting produced 5644 plants, in addition to the seed collected.

Since 1980, the Mason Tree Nursery has expanded production to 38 different forb species, and is now planting about 25 species each year (Table 1). In 1983, 35,000 plants were obtained from 596 m^2. In addition, seed collection areas have been established for 36 species (Table 2).

Missouri

In 1983, after visiting the Mason Tree Nursery the Missouri Department of Conservation initiated a similar project at the George O. White State Forest Nursery at Licking, Missouri. Seeds of several species were hand collected from public prairies and fall planted at the nursery in 828 m^2 (9000 ft^2) of seedbed (Table 3). Several species of legumes were stratified over winter and spring planted. Seeding was done with a precision garden seeder, with four rows per bed. Subsequent plantings will be done with a standard tree seeder with eight rows per bed. All species except *Asclepias tuberosa* germinated, though germination rates were low for several

TABLE 1. Mason Tree Nursery forb production: planting methods, rates, number of plants produced and amount of seed harvested.

Species	Planting Method	Planting rate: oz/100 ft^2	Plants produced per 100 ft.	Lbs. seed per 100 ft.
Amorpha camescens	drill	8.5	900	
Asclepias tuberosa	hand	2.5	*	*
Aster laevis	hand	3.5	9,300	9.5
A. novae-angliae	hand	3.5	3,600	21.0
Baptisa leucantha/leucophaea	drill	26.5	250	*
Camassia scilloides	hand	3.5	**	**
Ceanothus americanus	drill	9.0	200	.31
Coreopsis palmata	hand	3.5	1,300	*
Coreopsis tripteris	hand	9.0	1,700	1.0
Desmodium illinoense	hand	10.0	*	2.5
Dodecatheon meadia	hand	3.0	**	**
Echinacea pallida	drill	6.5	2,600	2.5
Eryngium yuccifolium	drill	5.5	2,100	3.75
Helianthus occidentalis	hand	6.5	1,300	5.25
Heliopsis helianthoides	drill	9.0	1,300	4.0
Hieraceum longipilum	hand	4 cups	700	1.25
Lespedez capitata	drill	9.0	130	2.25
Lespedeza leptostachya	hand	10.0	1,600	2.0
Liatris aspera	hand	6.5	3,800	20.0
L. pycnostachya	hand	6.5	7,300	10.5
Parthenium integrifolium	hand	10.0	1,700	*
Petalostemon candidum	drill	12.5	600	4.0
P. purpureum	drill	10.5	600	2.25
Physostegia virginiana	hand	1.5	2,500	*
Potentilla arguta	hand	0.5	900	1.25
Prenanthes aspera	hand	13.5	600	4.25
Ratibida pinnata	drill	9.0	1,000	6.5
Rosa carolina	drill	13.5	65	*
Rudbeckia subtomentosa	hand	1.25	*	*
Silphium integrifolium	hand	12.5	**	**
S. laciniatum	hand	13.5	1,500	*
S. terebinthinaceum	hand	11.0	3,000	*
Solidago rigida	hand	8.5	200	*

*Information insufficient to determine amounts, though all species survived.
**Planted in fall 1983, results not available.

species. Results exceeded expectations considering that seeds were collected during severe drought conditions in 1983. All but three of the species bloomed the first year (Table 3). Plans for 1984 include the addition of 13 species and 920 m^2 of seedbed. As in Illinois, plants will be grown for two seasons and the seeds will be harvested by hand before seedling distribution.

TABLE 2. Forb species established in seed collection areas at Mason Tree Nursery, Topeka, Illinois.

Amorpha canescens
Asclepias tuberosa
Aster laevis
A. novae-agliae
Baptisia leucantha
B. leucophaea
Camassia scilloides
Ceanothus americanus
Coreopsis palmata
Coreopsis tripteris
Despodium canadense
D. illinoense
Dodecatheon meadia
Echinacea pallida
Eryngium yuccifolium
Helianthus occidentalis
Heliopsis helianthoides
Hieracium longipilum
Lespedeza capitata
Lespedeza leptostachya
Liatris aspera
L. pycnostachya
Parthenium integrifolium
Petalostemon candidum
P. purpureum
Polytaenia nuttallii
Potentilla arguta
Prenanthes aspera
Ratribida pinnata
Rosa carolina
Rudbeckia subtomentosa
Silphium integrifolium
S. laciniatum
S. terebinthinaceum
Solidago rigida
Traderscantia ohiensis

DISCUSSION

It is important to keep in mind that the primary purpose of state forest nurseries is tree production. Nursery personnel are tied up with lifting and distribution of tree seedlings during winter and spring, leaving fall available for work with prairie plants. Fall seeding works well for all the forb species planted in Illinois and Missouri, eliminating the need for stratification. Two year old forbs are lifted from the nursery beds in the fall using a machine designed to lift tree seedlings. The bare root plants are packed in moist sphagnum and shipped via UPS to prairie restorations for transplanting by agency personnel. This treatment appears to be successful, though no comprehensive data have been collected regarding seedling survival. Preliminary counts from four Illinois restoration projects indicate survival rates from 0 to 100% with an average of 73.6% for all species on all sites (Table 4). It is

TABLE 3. Forb species planted at George O. White State Forest Nursery, Licking Missouri.

Amorpha canescens
Baptisia australis
**Callirhoe digitata*
**Echinacea pallida*
**Eryngium yuccifolium*
**Liatris pycnostachya*
**Petalostemon candidum*
**P. purpureum*
**Silene regia*
Silphium laciniatum

*Flowered first season.

TABLE 4. Survival rates of fall planted 2 year old seedlings in Illinois.

	Wolf Creek		Funk's Grove		Weldon Springs				All Areas	
					Bottomland		Upland			
	T	%Survival	T	%Survival	T	%Survival	T	%Survival	T	Survival
Amorpha canescens	17	100	14	67	1	100	8	100	40	90
Petalostemon sp.	17	94	17	94	-	-	-	-	34	94
Silphium terebinthinaceum	19	58	29	86	6	17	2	0	56	66
Aster laevis	18	61	-	-	-	-	6	83	24	67
Silphium integrifolium	4	100	-	-	-	-	-	-	4	100
Liatris pycnostachya	61	90	83	96	14	100	12	100	170	95
Heliopsis heliantoides	12	8	10	40	-	-	3	100	25	32
Eryngium yuccifolium	44	75	50	90	13	77	13	69	120	81
Echinacea pallida	36	0	42	31	5	60	2	100	85	21
Solidago rigida	-	-	10	90	-	-	1	100	11	91
	228	65	255	79	39	74	47	85	569	73.6%

T = total number of individuals planted.

possible that mortality is related more to planting techniques than distribution methods or timing.

Conformance to nursery techniques and equipment also dictates to some extent which species can be grown. Several species have been dropped from seedling production at the Mason Tree Nursery. *Coreopsis tripteris, Solidago rigida* and *Ratibida pinnata* have been dropped because their matted root systems make separation of plants at the time of lifting virtually impossible.

The advantages of producing prairie grasses and forbs at state forest nurseries make up for any inconveniences pertaining to timing or species grown. The most significant factor is cost. In 1983, the Mason Tree Nursery estimated a cost of $84/kg ($38/lb) for the 112.5 kg (248/lb) of seed collected. The average cost per kilogram of the same species if purchased from a commercial source was estimated to be $224 ($102/lb). At 112.5 kg of seed collected, that translated to a savings of $25,000. The average cost of seed collected in Missouri also averaged about $84/kg.

Missouri's experiences with direct-seeding forbs in native warm season grass plantings has been poor at best for several species including *Silphium laciniatum* and *Liatris pycnostachya*. The reasons for this are unclear but may be related to competition from the warm season grass seedlings and/or a spring planting date. Germination of these species at the White Nursery has been excellent, however. In any event, raising some forbs in a nursery setting for later transplanting results in maximum survival of plants per unit of seed. Preliminary results in Illinois indicate that at least *S. laciniatum* transplants well (Table 4). As a result, in addition to a savings in cost per pound of seed, there is a cost savings in terms of the number of plants surviving per pound of seed as well.

In addition to cost, another benefit is availability of species. Of 23 species planned for planting in Missouri in 1984, only 13 are available commercially. In addition, Missouri presently has no commercial sources of Missouri ecotype plant materials. The majority of material used in the Department's native warm season grass program comes from Nebraska and Kansas. Gardeners interested in growing native wildflowers obtain plants from sources in Illinois and Wisconsin. Species native to Missouri are available from these sources, however Missouri ecotypes are not. In Illinois, where there are several commercial sources, seeds of some species are either not commercially available or not in desired quantities.

Since no commercial wildflower seed or plant sources presently occur in Missouri, the plants grown at the White Nursery will be made available to a variety of agencies and individuals. The majority of plants being grown are for use in the Department's warm season grass plantings and several prairie restorations being used for interpretation. Materials will also be used in landscaping at Department offices and visitor centers. Some materials will be made available to city and county parks departments interested in naturalizing areas within parks. Ultimately, the Missouri Department of Conservation hopes to provide "prairie plant bundles" to the public at a minimal cost, similar to the various tree bundles distributed from the nursery. This would encourage the use of native Missouri materials in private prairie restorations, warm season grass plantings and individual gardens. The Mason Tree Nursery will continue to produce plants for use only in Illinois Department of Conservation projects, since plants and seeds of native ecotypes are available to the private sector from several local commercial nurseries.

CONCLUSIONS

As state conservation agencies become more involved in prairie restoration efforts, their state forest nurseries can fill the need for native ecotype plant materials. A trained labor force exists in the nursery personnel, and the nurseries have the equipment necessary to handle the seeds and plants. Also, the prairie plants can be grown on a schedule that conflicts only minimally with existing nursery programs.

The advantages of nursery grown plants or seed are several. Plants and seeds of desired species may not always be available commercially, or if available, not in the quantities desired. In addition, there is a considerable financial incentive, with an average savings of $140/kg of seed.

Finally, and most important, growing plants at the state nurseries enables the use of native plant materials in restoration and revegetation projects, so that other potentially aggressive ecotypes might not be introduced.

MOWING AS AN ALTERNATIVE TO SPRING BURNING FOR CONTROL OF COOL SEASON EXOTIC GRASSES IN PRAIRIE GRASS PLANTINGS

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Abstract. The effects of spring mowing and burning were compared with an undisturbed control in a seven year old planting of five warm season prairie grasses: big bluestem (*Andropogon gerardi*), little bluestem (*Andropogon scoparius*), side oats grama (*Bouteloua curtipendula*), switchgrass (*Panicum virgatum*), and Indiangrass (*Sorghastrum nutans*). Cool season grasses present were quackgrass (*Agropyron repens*), meadow fescue (*Festuca elatior*), and Kentucky bluegrass (*Poa pratensis*). Biomass clippings were taken on each treatment twice during the growing season, on July 2-3 and August 20-22. Frequency studies were conducted on each treatment in autumn. Burning reduced total cool season grass production an average of 78% for both clipping dates, compared to the control. Mowing averaged a 48% reduction. Burned and mowed treatments exhibited significantly lower cool season grass production than the control for the July clipping. Total warm season grass production was 42% higher and 12% higher for the mow and burn respectively, for the July clipping. By late August, warm season grass biomass was highest on the burn and lowest on the mow. The differences found in warm season grass production between treatments were not significant for either clipping date. Frequency of big bluestem was higher on the burned than on the mowed or control plots. Little bluestem and side oats grama were more frequent on both the mowed and burned plots when compared to the control. Frequency of cool season grasses did not differ between treatments, except quackgrass was significantly less frequent in the burned plot. Quackgrass biomass was significantly lower on mowed and burned plots for the July clipping compared to the control. Four broadleaf weeds and one annual grass occurred at higher levels on the burned treatment, but were a minor component of total production.

INTRODUCTION

One of the most common problems in prairie establishment and maintenance in the Midwest is the control of exotic cool season perennial grasses. Cool season grasses generally begin growth a month earlier than most native prairie species and often cause severe competition problems in the early part of the growing season. This is particularly true in the Upper Midwest where cooler spring and summer temperatures predominate.

The use of fire is presently the prairie manager's most effective tool for controlling these undesirable grasses. Numerous studies of Midwestern prairies have documented the effectiveness of spring burning in reducing the vigor of cool season exotics while stimulating earlier growth and increasing flowering of warm season prairie species (Curtis and Partch 1948, Ehrenreich 1959, Hadley and Kieckhefer 1963, Svedarsky and Buckley 1975). Many investigations have been conducted to determine the causal factors that make spring burning so effective in this respect. The consensus is that the removal of dead mulch is the primary factor involved (Curtis and Partch 1950, Rice and Parenti 1978, Weaver and Rowland 1952). Denuding the soil surface increases the available light at ground level and encourages earlier and more rapid soil warming. The resultant higher soil temperatures favor the growth of warm season prairie species. This effectively lengthens their growing season while shortening that of cool season species (Henderson 1982, Hill and Platt 1975).

In addition to altering the soil environment, mid to late spring burning also causes physical damage to cool season grasses that have already initiated growth. Still-dormant warm season prairie species remain unharmed below the soil surface. This is particularly important in young plantings where prairie species are just becoming established and frequently experience strong competition from cool season exotics. A single well-timed burn can often tip the scales in favor of the prairie species and change the entire aspect of a planting.

Unfortunately, burning a prairie or a prairie planting is not always possible, due to insufficient fuel, local burning restrictions, or unfavorable spring weather. In such cases alternative management methods must be employed. The use of mowing to simulate the effects of burning is one option. A number of investigators report increased production in tallgrass prairies by mowing and raking at the end of the previous growing season or in spring before the initiation of new growth (Hulbert 1969, Penfound 1964, Vogel and Bjugstad 1968). An Illinois prairie mowed and raked in late April also showed a significant decrease in the production of two undesirable cool season grasses, Kentucky bluegrass (*Poa pratensis*) and smooth brome (*Bromus inermis*) (Old 1969).

The literature indicates that mowing is a viable alternative to burning in the management of Midwestern prairies. This has important implications for vegetation managers and particularly for the urban prairie landscaper who is usually restricted by law from utilizing fire. This paper presents preliminary data comparing the effectiveness of mowing versus burning to control introduced cool season grasses and to encourage early spring growth of prairie species. Although conditions will vary from planting to planting, the ecological concepts presented here have applications in a variety of situations. Hopefully this information will help in effectively managing prairie plantings when the use of fire is precluded.

METHODS

The study area is located within the University of Wisconsin - Green Bay Cofrin Memorial Arboretum. Green Bay is situated on the northeasternmost edge of the original prairie-oak savanna region of Wisconsin. A variety of prairie species can be found in small remnants in the surrounding area.

The study area has a modified continental climate. The waters of Green Bay prevent the occurrence of extreme summer temperatures. Mean maximum temperatures for the summer months range from 24° to 27° C and daily maxima rarely exceed 35° C. The average frost-free growing season is 153 days. Mean annual precipitation is 71 cm, with sixty percent occurring during the growing season.

The soils in the study area are eroded Kewaunee sandy loams, overlying fine sandy clay loams. Measurements of texture, pH, and organic carbon were made of the topsoil and subsoil, to a depth of 60 cm.

In 1974, five warm season prairie grasses of Nebraska origin were planted in the study areas on 2.8 hectares of former agricultural fields. These grasses were "Champ" big bluestem (*Andropogon gerardi*), "Aldous" little bluestem (*Andropogon scoparius*), "Butte" side oats grama (*Bouteloua curtipendula*), "Nebraska 28" switchgrass (*Panicum virgatum*), and "Holt" Indiangrass (*Sorghastrum nutans*). The planting was left undisturbed for six years. Annual and biennial weeds were common in the first few years, but had almost disappeared by 1980. At this point switchgrass had become the dominant species and a mulch 20-30 cm deep had developed. Three introduced cool-season perennial grasses, quackgrass (*Agropyron repens*), meadow fescue (*Festuca elatior*), and Kentucky bluegrass had now become the pre-dominant undesirable species.

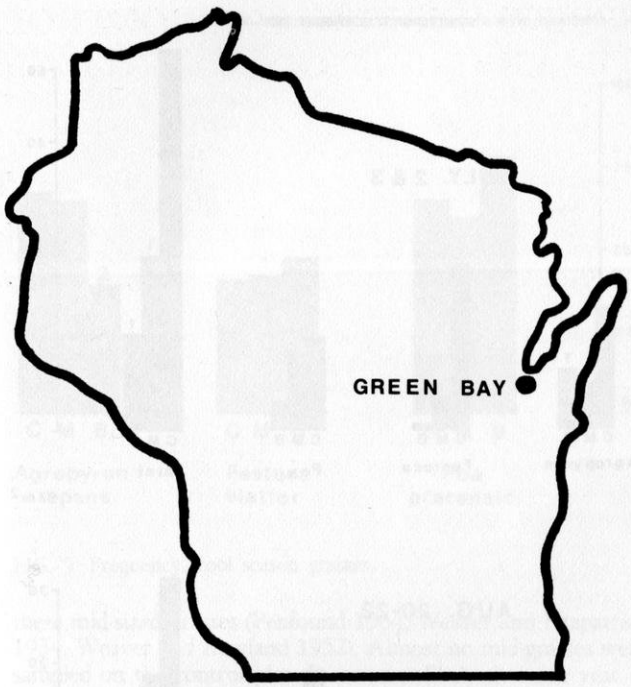

FIG. 1. Location of study area within the state of Wisconsin.

To evaluate the effects of burning and mowing on these species, three ten meter wide and fifty meter long transects were laid out in spring of 1980. Treatments were as follows:

CONTROL (C) - Not Burned or Mowed
MOW (M) - Mowed and Raked, May 1, 1980
BURN (B) - Burned, May 15, 1980

The control was left untreated. The mowed transect was cut with a flail mower, leaving a stubble approximately 5 cm high. The mowed material was removed using garden rakes. The burned transect was backfired two weeks after mowing. The fire essentially consumed all living and dead material on the plot.

To measure the response of individual plant species to each treatment, biomass clippings were taken on July 2nd and 3rd and on August 20-22. The July date was chosen to estimate maximum cool season grass production. The late August clipping was used to estimate maximum production of warm season grasses. Ten 0.1 m_2 quadrats were clipped every five meters along the control and mowed transects, and nine were clipped on the burn due to its slightly shorter length. The clipped plant material from each quadrat was separated by species, dried in an oven at 95° C for 24 hours, and weighed. All residual dead plant material was collected, dried and weighed. Analysis of variance was used to evaluate the results of the biomass studies.

Presence studies were conducted on October 31 and November 1, 1980 to compare frequency of all species in each treatment. One hundred samples were taken on each of the three treatments using a 0.1 m^2 quadrat. Chi-square calculations were used to determine differences in occurrences of each species by treatment.

RESULTS AND DISCUSSION

The most striking difference among the three treatments was the presence of a thick mulch on the control plot throughout the growing season. At the time of the early July clipping the control averaged 931 g/m^2 of dead litter. This compared to 147 g/m^2 on the mow (mostly stubble) and only 6 g/m^2 on the burn. In late August the control lost some mulch due to decomposition, but 659 g/m^2 still remained. The mow and burn each averaged 26 and 21 g/m^2 of litter at this time, respectively.

Although soil temperatures were not taken in this study, it is presumed that the control plot experienced lower spring soil temperatures than the mowed and burned sites. Peet et al. (1975) found daytime surface soil temperatures on a burned Wisconsin prairie to be as much as 20° C higher than adjacent unburned areas in mid-May. Brown (1967) recorded daily mid-May soil temperature gains on a burned Wisconsin prairie that exceeded those of unburned areas by as much as 85%. Little difference in energy dynamics would be expected between the burned and mowed areas once the litter was removed. Old (1969) found that spring surface temperatures on mowed and raked plots did not deviate by more than 1° C from burned plots on an Illinois prairie. Steiger (1930) and Hulbert (1969) compared spring soil temperatures on burned prairies to mowed and raked prairies. No significant differences were found in their studies. Removal of mulch by spring burning or mowing results in more rapid soil warming at similar rates compared to mulched surfaces.

Warm Season Grasses

Total warm season grass production in early July was greatest on the mowed transect, with 283 g/m^2. The burn and control produced 224 and 200 g/m^2, respectively. Warm season grass biomass was 42% higher on the mow and 12% higher on the burn compared to the control, but no significant differences between treatments were found. Increased grass production on the mowed plot compared to the burned plot in July is attributed to mulch removal 14 days earlier on the mowed plot. This allowed the soil to warm up sooner and stimulated earlier growth of the prairie grasses. Studies in Wisconsin (Brown 1967), Iowa (Ehrenreich 1959) and Nebraska (Weaver and Rowland 1952) show that differences in soil temperature between heavily mulched, undisturbed prairies and burned or mowed and raked prairies tend to disappear by mid-June or early July. New plant growth on denuded areas shades the ground, equalizing soil temperatures and consequently, growth rates. The earlier mulch is removed, the greater the proportional advantage there is in the form of increased spring growth.

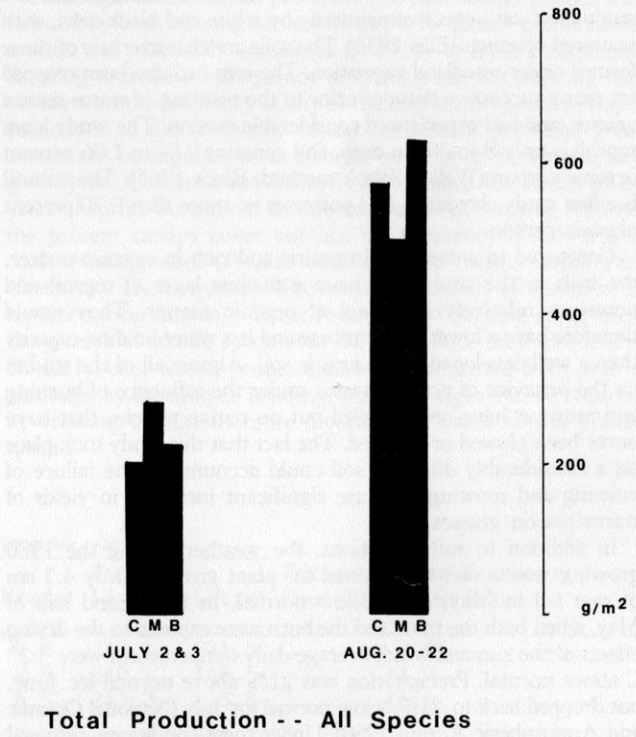

FIG. 2. Biomass, warm season grasses.

By late August, total warm season grass production was greatest on the burned treatment, with 632 g/m². The mowed plot exhibited the lowest production with 501 g/m², and the control was intermediate at 572 g/m². As in July, there was no significant difference between treatments. The mowed plot produced less than the control by late August, despite its larger crop of warm season grasses earlier in the season. Similar situations have been documented in states farther to the west. Ehrenreich and Aikman (1963) in Iowa and Hensel (1923a) in eastern Kansas found that plots that had mulch removed by spring burning showed higher spring and early summer production than unburned plots. During the latter part of the season, however, the unburned plots produced more than the burned, and total production by the end of the year was similar.

In a seven year study in eastern Kansas, Aldous (1934) found that native bluestem grasslands, burned in early spring, produced less total forage than unburned plots or plots that were burned later in spring. These results were attributed to lower soil moisture levels found in the early spring burned plots. The earlier removal of mulch contributed to greater moisture loss due to evapotranspiration and caused a reduction in infiltration of precipitation. This tended to limit growth of prairie grasses in the hot mid-summer months.

Most studies of tallgrass prairies on mesic soils show significant increases in total production of warm season prairie grasses in response to spring burning or mowing (Iowa - Aikman 1955, Hill and Platt 1975; Illinois - Hadley and Kieckhefer 1963, Old 1969; Missouri - Kucera and Ehrenreich 1962; Wisconsin - Brown 1967, Peet et al. 1975). Although other studies report that burning or mowing does not significantly increase production (Iowa - Ehrenreich and Aikman 1963; Kansas - Anderson 1964, Hensel 1923b; Missouri - Ehrenreich 1959), these investigations were conducted in climates more arid than Wisconsin. It is thus surprising to find no significant increase in production from burning or mowing in this study in Wisconsin.

An explanation of this phenomenon may be found in the nature of the soils on the study site. These soils did not develop under prairie, and do not possess the typical deep, rich profile of a prairie soil. The original surveyor's records of 1834 indicate that the study area was vegetated primarily by white and black oaks, with scattered openings (Ellis 1834). The soils are characteristic of those formed under woodland vegetation. The area had also been cropped for many successive decades prior to the planting of warm season grasses, and had experienced considerable erosion. The sandy loam topsoil is only 8 to 20 cm deep, and contains 0.84 to 1.06 percent organic carbon (Walkey Black method; Black 1965). The subsoil is a fine sandy clay loam, and possesses no more than 0.20 percent organic carbon.

Compared to a deep virgin prairie soil rich in organic matter, the soils in the study area have a shallow layer of topsoil and possess a relatively low level of organic matter. They would therefore have a lower nutrient base and less water-holding capacity than a well-developed mesic prairie soil. Almost all of the studies on the behavior of prairie grasses under the influence of burning and mowing have been carried out on native prairies that have never been plowed or cropped. The fact that this study took place on a considerably different soil could account for the failure of burning and mowing to cause significant increases in yields of warm season grasses.

In addition to soil conditions, the weather during the 1980 growing season was not optimal for plant growth. Only 4.5 cm of rain fell in May, 43% below normal. In the second half of May, when both the mow and the burn were exposed to the drying effects of the sun and wind, average daily temperatures were 3.2° C above normal. Precipitation was 21% above normal for June, but dropped back to 43% below normal for July (National Oceanic and Atmospheric Admn. 1980). Under these conditions, removal of mulch from the soil surface may not have been beneficial for plant growth. This could have been an additional factor in the

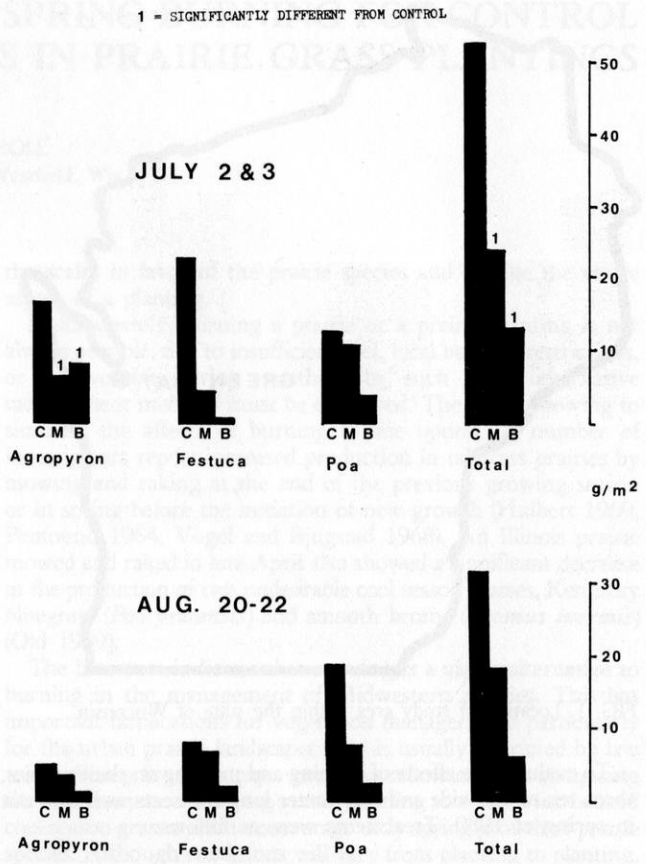

FIG. 3. Biomass, cool season grasses.

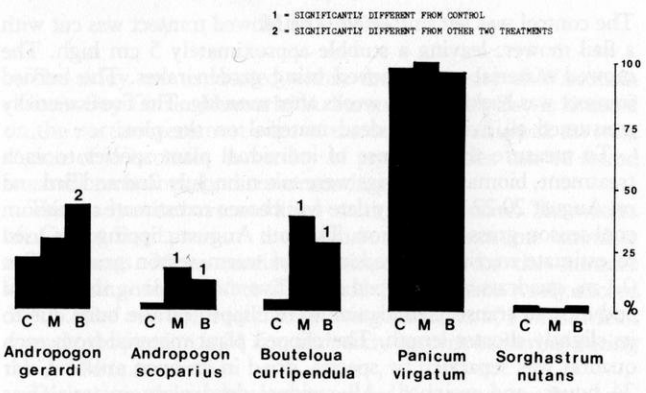

FIG. 4. Frequency, warm season grasses.

failure of burning and mowing to significantly increase production of prairie grasses.

The frequency of three warm season grasses appeared to be influenced by the mowing and burning treatments. Big bluestem was significantly more frequent on the burned plot than on the control or mowed plot. Similar results have been documented on eastern Kansas tallgrass prairies (Anderson et al. 1970, Hulbert 1969, McMurphy and Anderson 1965). Little bluestem and side oats grama both exhibited significantly higher frequencies on the burned and mowed plots. Plants of these two species were not well-developed, however, and accounted for only a small percentage of total warm season grass biomass on any treatment. The accumulation of mulch over the years had undoubtedly suppressed

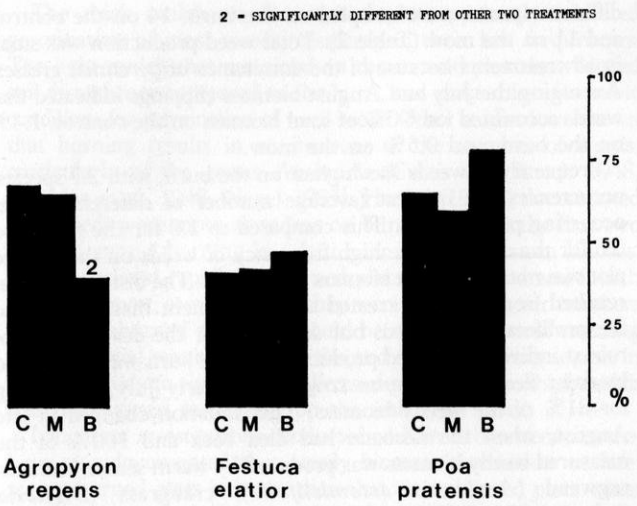

FIG. 5. Frequency, cool season grasses.

these mid-sized grasses (Penfound 1964, Weaver and Fitzpatrick 1934, Weaver and Rowland 1952). Almost no mid-grasses were sampled on the control plot. It seems unlikely that one year of mowing or burning would lead to such large increases in the frequency of any given perennial prairie grass. It is probable that the great majority of the mid-grasses found on the burned and mowed plots were remnants from earlier years, prior to the development of a thick mulch. The paucity of mid-grasses on the control raises the possibility that a large proportion of the plants sampled on the burned and mowed plots may have been in a state of dormancy, and were stimulated to renew growth by the removal of mulch.

Cool Season Grasses

Production of cool season grasses was highest on the control plot for both clipping dates. In early July the control averaged 53 g/m² compared to 24 g/m² for the mow (55% less) and 13 g/m² for the burn (75% less than the control). Analysis of variance showed that both the mowed and burned plots had significantly less production than the control for the July clipping.

Growth of cool season grasses is reduced during the summer in Wisconsin, and much of the spring growth dies back. Late August biomass surveys indicated a drop in total live standing crop on all three plots. Yields were 32, 18, and 6 g/m² for the control, mow and burn, respectively. Compared to the control, there was 44% less cool season biomass on the mowed plot and 81% less on the burned plot. Despite these notable reductions, large variations between quadrats obscured any statistical differences between treatments for the August clipping.

Burning reduced total cool season grass production an average of 78% for both dates compared to the control. Mowing averaged a 48% reduction. Burning caused a greater reduction than mowing because of two primary factors:

1. Burning is inherently more effective than mowing at removing above-ground growth. It essentially eliminated all organic material above the soil surface, while mowing left a 5 cm stubble which included some photosynthetic material.
2. Mowing was done on May 1, while burning occurred on May 15. This allowed the cool season grasses on the mowed plot two weeks longer to recover than those on the burn before the plots were sampled in early July.

Lower cool season grass production might be expected if mowing had been done at the same time as burning. The results of this study represent a conservative estimate of the relative effectiveness of mowing compared to burning in the control of exotic cool season grasses.

One method of evaluating the effectiveness of burning or mowing in prairie management is to compare the ratio of warm season to cool season grass production on each treatment. This number provides an index of the relative importance of the two with respect to each other. The ratio of warm season to cool season grasses is of greatest importance in spring and early summer, when cool season grasses are most active and present the most serious competition. Table 1 shows the relative effects of mowing and burning on the composition of the vegetation. Compared to the control, the ratio of warm season to cool season grass production in early July is more than three times higher on the mow and nearly 4 1/2 times higher on the burn. These ratios indicate that the effects of mowing and raking are similar to the effects of fire on the vegetation.

Quackgrass was the only cool season grass to exhibit a significant reduction in biomass due to treatment. Both mowing and burning lowered total production of quackgrass in the early July clipping. Meadow fescue and Kentucky bluegrass also appeared to be reduced by burning and mowing; however, great variability between quadrats resulted in large statistical variances that offset any differences in means between treatments.

Although total biomass production of cool season grasses was reduced by both burning and mowing, the frequency of individual species was practically unaffected by either of these treatments. Burning reduced the frequency of quackgrass, but mowing had no effect on the frequency of any of the cool season grasses. Major reductions in the frequency of any herbaceous perennial grass should not be expected from a single burning or mowing in any given year. Anderson and Bailey (1980) studied the effects of 24 years of spring burning in an Alberta parkland. Burning reduced the percent canopy cover but not the frequency of two major cool season grasses (*Festuca scabrella* and *Stipa spartea* var. *Curtiseta*). The frequency of both species actually increased with regular spring burning. These results show burning suppressed the growth of certain species but did not reduce their frequency. Similarly, cool season exotics cannot be eliminated from prairie plantings by burning or mowing, but their vigor can be reduced by creating conditions more favorable to warm season prairie species.

TABLE 1. Average biomass production by treatment and clipping date.

Clipping Date	Treatment	No. of Quadrants	Grams Dry Wt./M² Warm Season Grasses	Cool Season Grasses	Weeds	Total Living	Litter	Ratio of Warm Season to Cool Season Grasses
July 2-3	Control	10	200.4	52.9	6.5	259.8	931.5	3.8
	Mow	10	283.2	24.1	2.9	310.1	146.5	11.7
	Burn	9	223.6	13.2	6.5	243.3	5.8	16.9
August 20-22	Control	10	572.1	31.8	20.9	624.8	658.7	18.0
	Mow	10	500.6	18.4	0.5	519.5	25.6	27.2
	Burn	9	632.0	5.9	0.8	638.7	20.7	107.1

TABLE 2. Frequency of all species sampled on control, mowed and burned plots.

Species	% Frequency Control	Mowed	Burned
Warm Season Grasses:	n=100	n=100	n=100
Andropogon gerardi	21	28	42
Andropogon scoparius	0	17	12
Bouteloua curtipendula	4	38	28
Panicum virgatum	98	100	96
Sorghastrum nutans	2	1	2
Cool Season Grasses:			
Agropyron repens	67	66	39
Dactylis glommerata	4	1	0
Festuca elatior	41	42	47
Poa pratensis	65	59	77
Weeds:			
Acalypha rhomboideus	1	0	0
Ambrosia artemisifolia	3	11	78
Aster sp.	1	3	22
Bromus japonicus	9	24	7
Capsella bursa-pastoris	23	22	31
Cirsium vulgare	3	4	0
Digitaria Ischaemum	0	0	8
Hypericum perforatum	3	0	1
Juncus sp.	0	0	1
Lotus purshianus	0	0	7
Oenothera biennis	2	0	0
Oxalis stricta	10	13	46
Panicum capillare	0	0	2
Polygonum aviculare	1	2	2
Potentilla simplex	1	0	0
Rudbeckia hirta	0	0	2
Setaria lutescens	3	9	37
Solidago sp.	0	2	0
Taraxacum officinale	3	7	26
Trifolium repens	1	6	4

The reduction in quackgrass by burning and mowing found in this study agrees with visual observations made by the author. The effects of burning versus mowing and raking were compared on a different prairie planting at the University of Wisconsin - Green Bay Cofrin Memorial Arboretum. This planting of prairie grasses and forbs was five years old and thoroughly infested with quackgrass. In an attempt to control the quackgrass, part of the planting was mowed to a height of 2-3 cm and raked clean in late April. Another part was burned two days later. A control plot was left unburned and unmowed for comparison. At the time of mowing and burning, quackgrass was 15 to 18 cm high and the warm season prairie grasses had not yet emerged. A few prairie forbs such as yellow coneflower (*Ratibida pinnata*), black-eyed Susan (*Rudbeckia hirta*), and lupine (*Lupinus perennis*) had initiated growth.

By late June, the mowed and burned areas were visually indistinguishable from one another. Many prairie grasses and forbs were growing vigorously on both plots and flowered throughout the summer. Quackgrass regrew to a height of about 15 cm. No flowering culms of quackgrass were present on either the burned or mowed areas. In contrast, quackgrass was the dominant species on the control and flowered profusely. Prairie species were greatly suppressed on the control, and very few flowered that year. The similarity in effect between burning and mowing were striking; the numerical data presented in this paper agree with these observations.

WEEDS

A number of annual, biennial and non-grassy perennial weeds were present in the study plots. In the frequency studies, 15 different species were sampled on the burn, 14 on the control, and 11 on the mow (Table 2). Total weed production was small in all treatments because of the dominance of perennial grasses. Averaging the July and August biomass clippings indicated that weeds accounted for 3.0% of total biomass on the control, 1.4% on the burn, and 0.5% on the mow.

Frequency of weeds was highest on the burn, with 2.7 species-occurrences per quadrat (average number of different species occurring per quadrat). This compared to 1.0 for the mow and 0.6 for the control. The high frequency of weeds on the burned plot was not reflected in biomass production. The disturbance that resulted from burning created an environment that encouraged the proliferation of weeds but did not favor the development of robust individuals. Weed production on the burn was dominated by daisy fleabane (*Erigeron strigosus*) in early July, accounting for 81% of the weedy biomass. This situation changed in late August, when the fleabane had died back and 100% of the measured weedy biomass was produced by warm season annuals: ragweed (*Ambrosia artemisiifolia*), crabgrass (*Digitaria ischaemum*), witchgrass (*Panicum capillare*) and yellow foxtail (*Setaria lutescens*).

The control had the lowest number of species-occurrences per quadrat, but exhibited the highest total weedy biomass. Several large individuals of *Lotus purshianus*, a warm season annual legume native to the Great Plains and adventive in the Midwest, accounted for 45% of the weedy biomass measured on the control in early July, and constituted 96% of the late August measurements.

Frequency of weeds on the mowed plot was more similar to the control than the burned plot (Table 2). Total weedy biomass was lowest on the mowed treatment for both clipping dates (Table 1). Japanese brome (*Bromus japonicus*) was predominant in early July, with 54% of the total. By late August it accounted for 32% of total weed production and was secondary in importance to warm season annuals.

Six weedy species exhibited significant differences in frequency due to treatment. Burning strongly favored ragweed and yellow foxtail. These two species accounted for 89% of the total weedy biomass measured on the burn in late August. Burning also led to significantly higher frequencies of two perennial weeds, yellow weed sorrel (*Oxalis stricta*) and dandelion (*Taraxacum officinale*), and an aster that was found only in the vegetative state and could not be positively identified. None of these three contributed significantly to the total weedy biomass on the burned plot.

The only weedy species to be favored by mowing was Japanese brome. Because it germinates fairly early in the spring, it fared better on the mow than on the burn due to the earlier and less drastic removal of vegetation by mowing. Fire likely destroyed most seedlings and created warmer soil conditions that presumably discouraged further germination.

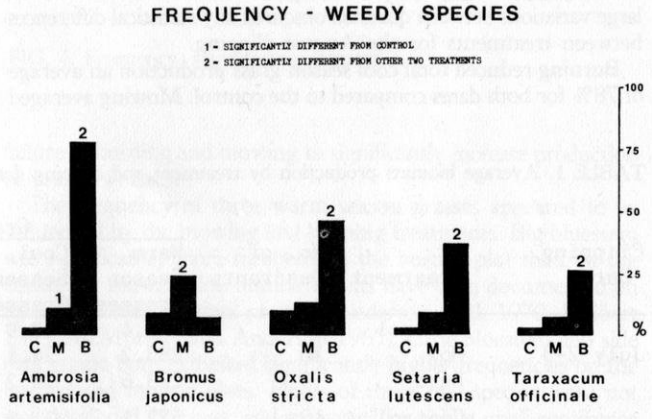

FIG. 6. Frequency, weedy species.

The thick mulch on the control plot apparently inhibited germination of most weeds, resulting in their low frequencies. The light mulch that remained on the mowed plot also reduced soil disturbance compared to the burn, and created less favorable conditions for germination of weed seeds. Other studies have shown that burning results in an increase in the number of weeds, particularly of the genus *Ambrosia* (Curtis and Partch 1948, Hopkins et al. 1948, Nagel 1983). Hensel (1923a) documented that weeds were more abundant on burned plots in the first two years of annual burning in a four year study in eastern Kansas. Weeds declined rapidly on burned plots in the third and fourth years, however, at which time they were found in lower numbers than on unburned plots. (It should be noted that most standing plant material was removed at the end of the growing season in Hensel's study to simulate the effects of grazing, and a thick mulch was not allowed to develop on the unburned plots).

Long-term investigations conducted on Kansas bluestem pastures have also documented that weedy biomass production on late-spring burned plots is lower than that on unburned plots when measured at the end of the growing season (Aldous 1934, Owensby and Anderson 1967). These results are similar to those obtained in this study, in which the end-of-season production of weeds on the control plot was many times that of the burn or mow (Table 1).

It is important to note that the study area in this investigation was dominated by perennial grasses that had developed a thick sod over a six year period. Their monopolization of the soil environment and foliar zone inhibited the development of many large, robust weeds. This is seldom the case, however, in young prairie plantings. The slow-growing native perennials typically do not occupy a large percentage of the soil during the first few years following seeding. Above-ground development of prairie grasses is restricted by annual weeds and cool season grasses, which account for a greater percentage of the total biomass. The mulch layer in a young prairie planting usually does not provide sufficient fuel to carry a fire. In the absence of burning, cool season grasses often attain dominance over prairie species by the second or third year. These early years are critical in determining the future composition of a prairie planting, but management options tend to be limited. In such situations, mowing in middle to late spring can be used to remove mulch and cut back undesirable cool season grasses. Good results can be obtained by using a heavy duty lawnmower, set as low as possible, with a bag attachment to collect the clippings. On large areas, a tractor-mounted rotary chopper can be used to cut standing material and blow it into a wagon for easy removal. This provides the vegetation manager with an alternative to burning to accelerate the growth of warm season prairie species in their early stages of development, and to reduce the accumulation of mulch in mature plantings when the use of fire is not feasible. Mowing also tends to create an environment that is less favorable for germination and growth of weeds compared to burning.

This study represents only one year of data collection, and the results must be viewed as preliminary. Follow-up investigations must be conducted to evaluate the long-term effects of mowing and burning on the vegetation.

ACKNOWLEDGEMENTS

Gratitude is expressed to Dr. David Jowett for his assistance with the statistics, to Dr. Keith White for his constant inspiration, to Cynthia Hypki for her insight and patience, and to Roseann Wallander for her invaluable assistance with data collection and processing.

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THE IMPACT OF DEER ON 24 SPECIES OF PRAIRIE FORBS

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Abstract. This 2-year study assessed the impact of herbivores on the condition and survival of 24 species of prairie forb seedlings in a newly-planted 5 hectare prairie. One hundred-twenty forbs were planted in each of six test and three control plots. Plants were monitored weekly to determine number of plants browsed, species selected, recurrence of browse damage, and general forb condition.

Only white-tailed deer browsed in test plots. Deer browsed selectively. Only 11 of 24 species were browsed the first year, and 12 the second year. Ten species were never browsed. *Aster azureus, Aster laevis, Helianthus giganteus, Helianthus rigidus*, and *Potentilla arguta* were selected most frequently. Most browsing occurred after seedlings were well established and primarily involved nipping off succulent stem tips. No plants were killed, and almost all continued to grow vigorously even when browsed more than once. Deer damage alone was not sufficient to severely impact seedling prairie forbs under the conditions of this study, where competition was limited and moisture was adequate.

INTRODUCTION

Hennepin Parks operates a 10,500 ha system of park reserves and regional parks just west of Minneapolis, Minnesota. Many of the Park District's grasslands have been managed for and restored to native prairie species during the past 10 years. Almost 250 ha have been planted to date. Early restoration efforts involved seeding uniform stands of grasses with the intent of introducing forbs at a later date. During the past 5 years, however, grasses and forbs have been seeded simultaneously, and seedling forbs have been transplanted into the area within 1 week of seeding at a rate of about 2500 per hectare.

Forb survival has been lower than expected. For example, 309 forbs were planted into established prairie grasses in the springs of 1981 and 1982. Only 35 of 209 forbs planted in 1981 and 70 of 100 forbs planted in 1982 were still visible in July 1982. Possible reasons for forb losses include:

1. Stress to the plant during transplant.
2. Plant desiccation in its new environment.
3. Competition for water and nutrients from annual weeds as well as prairie vegetation, and
4. Browsing by mammals, both above and below ground.

Efforts have been made to control the first three factors, but no attempt has been made to control browsing.

There has been a dramatic change in wild herbivore populations using the grasslands of Minnesota during the past 200 years. The large migratory grazing species such as elk (*Cervus canadensis*) and bison (*Bison bison*), which have a distinct preference for grasses (Hobbs 1979, Hunt 1979, Peden 1976), have been replaced by edge-dwelling species like the white-tailed deer (*Odocoileus virginianus*) and eastern cottontail (*Sylvilagus floridanus*), which prefer to eat forbs (Dasmann 1981, Kohn 1971, Korschgen 1980). This transition to edge-dwelling mammals is becoming increasingly problematic as the size of Minnesota's prairie tracts is diminishing. More prairie remnants are adjacent to urban settings or woodlots, and the number of herbivores is often not controlled.

Park District personnel suspected that herbivores were having a detrimental effect on the condition and survival of seedling forbs transplanted to newly-seeded areas. Therefore, our project objective was to assess the impact of browsing by wild mammals on seedling forb condition and survival in newly established prairie restorations. We wished to determine which mammals were selecting which forb species and with what frequency.

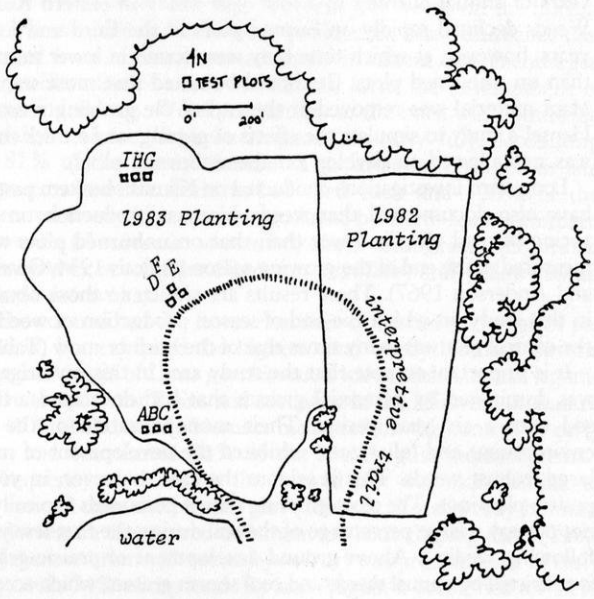

FIG. 1. Study site and test plots.

STUDY AREA

The 5 ha study area is located at Hyland Lake Park Reserve, Bloomington, Minnesota, just southwest of Minneapolis. The area was originally prairie, but was converted to cropland for almost half a century before it was seeded to brome grass in the early 1960's. The study area is bordered by woods to the north, sumac and early-succession woody growth to the south and west, and a 4 ha open area to the east, which was plowed and seeded to prairie species in 1982 (Fig. 1). Housing developments surround the park reserve.

METHODS

In the fall of 1982, the study area was sprayed with Roundup herbicide. In the spring of 1983, it was plowed, disked, and seeded to native forbs and grasses using a Truax Drill. Seedling forbs were then transplanted into the area within 1 week of seeding at a rate of about 2500 per hectare.

Three study sites were located in the newly-seeded area, one near the sumac in the south end, one in the center of the planting, and one near the oak woods on the north end (Fig. 1). In order to evaluate mammal use of the study area, three test plots were established at each study site as follows:

1. One plot excluded all mammals: A 5 m x 5 m area was enclosed with 2.4 m high fence, with hardware cloth (1 cm mesh) sunk 10 cm into the ground and fastened to the bottom of the fencing.
2. One plot allowed small mammal access only: A 5 m x 5 m area was enclosed with 2.4 m high fence, which was raised to leave a 20 cm space at ground level.
3. One plot allowed both small mammal and large mammal access: A 5 m x 5 m area was staked, but left unfenced.

TABLE 1. Prairie forb species and number of individuals browsed in three 25 m² unfenced plots.

Species	1983 No. browsed/total	1983 Percent	1984 No. browsed/total	1984 Percent
Allium stellatum Ker.	0/12	0	1/09	11
Agastache foeniculum (Pursh) Kuntze.	3/14	21	0/14	0
Aster azureus Lindl.	14/15	93 *	8/14	57 *
Aster laevis L.	14/14	100 *	5/12	42 *
Helianthus giganteus L.	8/15	53 *	6/15	40 *
Helanthus rigidus Rydb., Small	12/15	80 *	2/14	14
Heliopsis helianthoides (L.) Sweet	0/13	0	2/13	15 *
Heuchera richardsonii R. Br.	0/15	0	2/13	15 *
Potentilla arguta Pursh	8/13	62 *	1/11	9
Ratibida pinnata (Vent.) Barnh.	7/15	47	2/15	13
Rudbeckia hirta L.	5/14	36	1/12	8
Solidago nemoralis Ait.	3/15	20	2/15	13
Solidago speciosa Nutt.	1/13	8	0/12	0
Verbena stricta Vent.	2/15	13	3/15	20 *
	77/198	39	35/184	19

* Most heavily browsed each year.

One hundred-twenty forbs (five each of 24 species) were planted randomly in the first test plot, and the same pattern was used in each of the remaining plots. The species differed considerably in their moisture and soil requirements, ranging from dry *Aster sericeus* to wet *Helianthus giganteus*. Soils ranged from well-drained gravel pockets to clay/sand mix.

Test plots were monitored weekly to determine the number of plants browsed, species selected, severity and recurrence of browse damage, and general condition of the forbs. Herbivore use of the test plots was determined through 24-hour observations of the study area, small mammal trapping, track observation, and examining each plant weekly to determine the method of browse damage (height that the bud, leaf, or stem was nipped off, and whether it was a clean bite, broken off, or ripped).

RESULTS

Browsing occurred only in the unfenced plots (C, F, and I). Although eastern cottontails and thirteen-lined ground squirrels (*Spermophilis tridecemlineatus*) were occasionally observed in the study area, none were trapped in the test plots, and no indications were found that they browsed any of the test species. The white-tailed deer was the only herbivore that actually browsed in the test plots. Winter aerial surveys indicated a population of about 12 animals per square km at Hyland (32 deer/mi²). The summer density is unknown, but as many as six deer were seen on the study area at one time.

Similar browse patterns occurred in all three test plots in 1983, and this pattern persisted in Plots C and F in 1984 (Fig. 2). The browsing pattern in Plot I, however, was modified significantly due to persistent use by a doe and fawn. This was probably due to the close proximity of the plot to the woods edge. Plot I received four times as much browse damage as Plot C or F in 1984. Five species were browsed that were not touched in any other plot during the year (*Allium stellatum* - 1 plant, *Heliopsis helianthoides* - 2, *Heuchera richardsonii* - 2, *Solidago nemoralis* - 2, *Verbena stricta* - 3). Three of these species were not browsed in any other plot at any other time in the study (*Allium stellatum, Heliopsis helianthoides*, and *Heuchera richardsonii*). Deer were very selective in the species they ate.

Eleven of 24 forb species were browsed the first year, and 12 the second year (Table 1). Ten species were never browsed (Table 2). The five species most heavily browsed each year are highlighted in Table 1.

Overall, 77 of 360 (21%) available plants of all species were browsed by deer in 1983, and 35 of 274 (13%) available plants were browsed in 1984. Twenty-three of the 77 individuals browsed in 1983 were also browsed in 1984, for a total of 89 plants receiving damage over the course of the 2-year study.

Individual plants were never browsed more than three times per season. Only the five species most frequently selected were browsed more than once.

Browsing did not significantly affect seedling forb survival. Most browsing occurred after seedlings were well established and involved primarily nipping off succulent stem tips. Fenced and unfenced plants survived equally well (Table 3). Only five of 89 damaged plants died by August 1, 1984, and browsing may not have been the cause. Desiccation and competition from surrounding plants also affected survival. One loss was due to human error while weeding.

Browsing did affect seedling forb condition, especially with those plants that were repeatedly browsed. Most browsed plants were shorter. Some had fewer flowering heads than their fenced counterparts. Some plants did not flower at all. *Aster azureus, Aster laevis, Helianthus giganteus, Helianthus rigidus*, and *Potentilla arguta* were most frequently and severely browsed. Most plants that were damaged in 1983 came back vigorously in 1984.

TABLE 2. Unbrowsed prairie forb species.

Amorpha canescens Pursh	*Penstemon gracilis* Nutt.
Anemone cylindrica Gray.	*Penstemon grandiflorus* Nutt.
Asclepias tuberosa L.	*Petalostemum purpureum* (Vent.) Rydb.
Aster sericeus Vent.	*Ratibida columnifera* (Nutt.) Woot. & Standl.
Coreopsis palmata Nutt.	
Echinacea angustifolia (D.C.) Cron.	

TABLE 3. Survival of 14 species of browsed forbs.

	All individuals		Fenced individuals		Unfenced individuals	
	No. browsed and survived/total	Percent	No. browsed and survived/total	Percent	No. browsed and survived/total	Percent
1983	604/630	96	407/420	97	197/210	94
1984	530/630	83	345/420	82	185/210	88

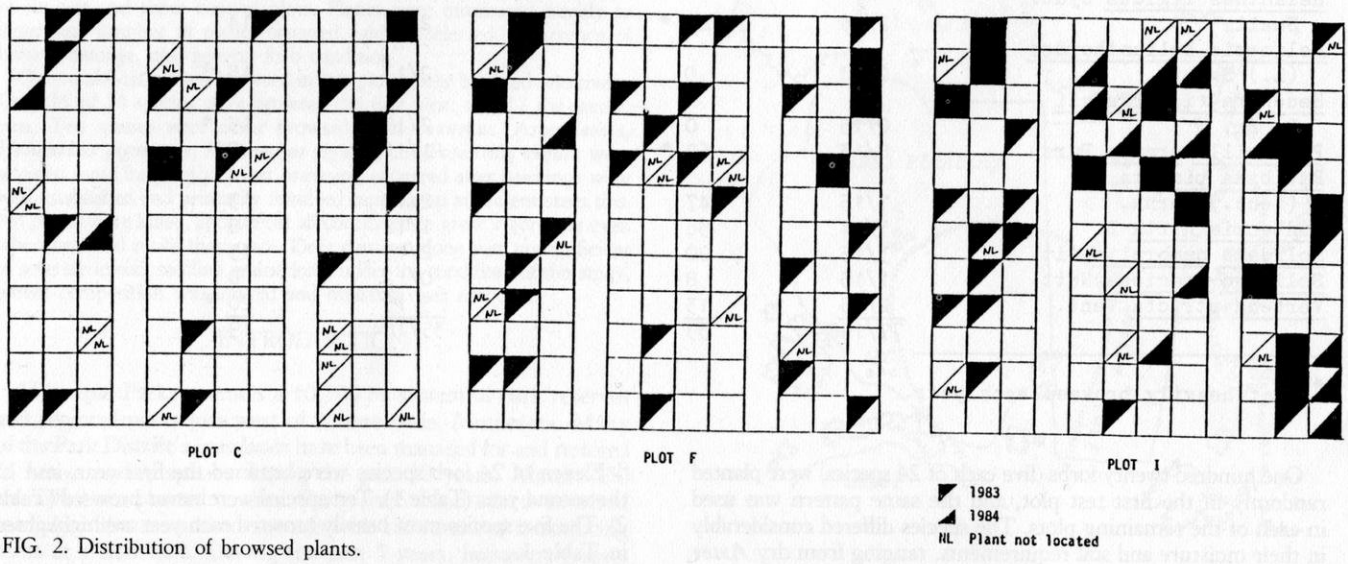

FIG. 2. Distribution of browsed plants.

Other factors were more important than browsing in determining seedling forb condition and survival during the course of the study. Moisture was adequate in both 1983 and 1984 to eliminate the need for supplemental watering in the test plots. Unfortunately, severe thunderstorms in 1983 inundated about one third of the plants in Plot C on three occasions, covering the seedlings with silt deposits. The plot was ditched to prevent further flooding. In addition, high winds accompanying rains in September flattened many of the fall-blooming plants, especially asters.

In 1984, high moisture levels were accompanied by luxuriant weed growth throughout the study area. Species included yellow sweet clover (*Melilotus officinalis*), velvet-leaf (*Abutilon theophrasti*), great ragweed (*Ambrosia trifida*), red clover (*Trifolium pratense*), and alsike clover (*Trifolium hybridum*). These weeds were especially bad in the northern test plots (G, H, and I), where they often formed a closed canopy within a week after weeding. In these plots, prairie plants grew thin and straggly. Some dry-site plants rotted off at ground level. On the other hand, this abundant growth of weeds outside the test plots provided additional food for deer, as evidenced by heavy browsing on velvet-leaf, sweet clover, and great ragweed. Some of the pressure on prairie forbs was thereby eliminated. Also, the canopy of weeds may have concealed some of the prairie forbs from the deer.

CONCLUSIONS

1. The white-tailed deer was the only mammal that browsed in the test plots. Other species were present in the study area in small numbers, but there were no indications that they used the test plots.
2. White-tailed deer were selective in the species they browsed.
3. Browsing by deer did not significantly affect forb survival under the conditions of this study.
4. Browsing by deer did affect forb condition.
5. Browse damage in Plot I adjacent to the oak woods was worse in 1984 due to repeated visits by one family of deer.
6. Other factors were more important than browsing in determining forb survival during this 2-year study.

Browsing by deer was not as important a factor in seedling forb survival as had been anticipated. However, browsing may be a significant factor under other environmental conditions. Both 1983 and 1984 were wet years in southern Minnesota. While weeds competed with prairie forbs for light and nutrients, they also reduced browsing pressure by providing an alternate food source for deer. Under drought conditions, newly-planted prairie forbs may provide the only succulent summer browse available. The number of species browsed, number of individuals browsed, and recurrence of browse may all be higher in drier years. Under dry conditions, heavily browsed plants may not be able to resume growth sufficiently to survive the winter or compete successfully with annual vegetation the following spring.

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LARGE SCALE SEED HARVEST OF NATIVE TALLGRASS PRAIRIE

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Abstract. The U.S. Fish and Wildlife Service, Minnesota Wetland Complex, began harvesting prairie seed mixture from native tallgrass prairie in 1979. This began largely because of concern over winter hardiness of many of the Nebraska-origin warm season native grasses that were then being seeded for waterfowl nesting cover. Prairies were harvested with an unmodified small grain combine using a straight cut header. The first year harvest yielded 193 kg PLS (Pure Live Seed) from 14.2 ha. The process was gradually perfected and increased to a 1983 harvest of 3,966 kg PLS. Through the 1983 harvest, 10,626 kg PLS were harvested from native prairie in Minnesota. An additional 567 kilograms PLS were harvested in North Dakota. Average yield for all Minnesota harvests was 11.8 kg PLS/ha, at an average cost of $4.94/kg PLS. State seed laboratories have identified more than 37 native species in the mixture. Eleven species have at times represented at least 1 percent of the mixture. *Andropogon gerardi* Vitman has nearly always been the dominant species. Germination plus dormant values exceeding 80 percent have not been uncommon.

INTRODUCTION

Harvesting of native prairies is not a recent development. During the 1930's, the U.S. Soil Conservation Service (SCS) first sought to harvest seed of tall, warm season native grasses from native prairies. This did not prove to be a reliable seed source because of low yields and poor seed fill in dry years. The SCS found that by developing or selecting superior varieties and by growing them under more ideal conditions, they could increase the quality and quantity of the few varieties of grasses chosen for reclamation use (E. Jacobson, USDA, SCS Plant Materials Center, personal communication). Even though much seed is still harvested from native grasslands, mostly in single species lots, most seed commercially available originated from SCS developed varieties. In 1978, before the U.S. Fish and Wildlife Service (FWS) began harvesting native tallgrass prairie, the only commercially available seed came from Nebraska-origin SCS and University of Nebraska developed varieties. The FWS initially used these varieties to establish upland nesting cover for waterfowl in northwestern Minnesota.

McMillan (1959) and others determined that the tall warm season grasses were genetically programmed to flower with a particular photoperiod and this requirement remained constant when an ecotype or variety was moved from its original location. Some varieties in use by FWS were flowering up to sixty days later than the local ecotype and winter injury frequently occurred in the establishment year in northwestern Minnesota. The FWS, Minnesota Wetland Complex, began harvesting a prairie seed mixture consisting primarily of big bluestem (*Andropogon gerardi* Vitman.) and Indiangrass (*Sorghastrum nutans* (L.) Nash.) in 1979. This began largely because of concern over winter hardiness of many of the Nebraska-origin varieties.

METHODS

Almost all prairies harvested were burned in the spring of the harvest year to improve seed yield. Burning increases the number of flowering culms of tall warm season native grasses, especially big bluestem (Daubenmire 1968, Olson 1975, Pemble et al. 1973) and also improves germination (Ehrenreich and Aikman 1957). In northwestern Minnesota the best seed yields have been obtained from prairies burned in late May or early June after initiation of warm season grass growth. One of the best yields of big bluestem was obtained from a prairie that was burned by June 17 wildfire. Another advantage to late spring burning is that undesirable cool season grass species, such as quackgrass (*Agropyron repens* (L.) Beauv.) and smooth bromegrass (*Bromus inermis* Leyss.), usually will not flower (Olson 1975).

Harvest dates ranged from September 10 to October 1. Generally the Indiangrass had started to shatter before harvest began. Most of the switchgrass (*Panicum virgatum* L.) had already shattered.

Prairies were harvested with an unmodified small grain combine using a straight cut header. Cutting height varied with the species being harvested. Generally the cutting height was adjusted to harvest shorter species whenever possible. Undesirable species where avoided by lifting the header or by driving around them. The combine most often used was a Massey Ferguson 760 with a 7.3 meter header, but most combines will work to various degrees. Combine adjustments generally were as follows: Cylinder speed - 800-1200 revolutions per minute; cylinder bars - close as far as possible; air - very slight but not shut off; sieves - all open at least 1.3 centimeters; ground speed - 8-11 km/hr. Most combines will not auger the coarse seed from the storage hopper; therefore, removal must be done with hand tools. An individual combine has harvested as much as 30 hectares per day.

The harvest material has a high moisture content and will heat up from bacterial action if not spread out to dry within a few hours. Drying has most often been done indoors in a building with a large dry floor. The seed should be spread to no more than 30 cm in thickness. For 3-5 days the seed should be turned or mixed at least twice daily to prevent heating and molding. This can be accomplished most easily by people shuffling their feet through the spread seed. After 5 days, mixing should be done at least on a daily basis until the seed is dry enough to emit dust upon mixing. After such time, the seed can be bagged and transferred for cleaning.

The SCS Plant Materials Center at Bismarck cleaned (debearded) some of the small lots in the early years of FWS harvest, but was unable to process the large quantities harvested later due to time constraints. One lot was commercially cleaned in 1980, but this company refused to do it again. Because local commercial seed cleaners are ill equipped to handle rough chaffy seed, the FWS installed a cleaner/scalper in 1982. The cleaner is a Crippon Model K 242GA with two large (107 x 137 cm) screens. Cleaning is a one-step process accomplished by running the material through both screens (top - 17.5 mm round; bottom - 15 mm round) and recovering the finished product from the bottom. Up to 300 kg/hr can be cleaned in this manner. The end product is sufficiently cleaned to work well in a Truax grass seed drill.

A seed sample is obtained from each cleaned bag of seed, mixed together, and a small subsample of that is sent to a state seed laboratory for analysis. Purity, germination and dormant values are obtained for those species comprising more than one percent bulk of the mixture. The seed is subject to both federal and state seed laws even if it is not intended for sale.

RESULTS

The Detroit Lakes Wetland Management District (WMD) conducted the first harvest in 1979 on The Nature Conservancy's (TNC) Bluestem Prairie near Moorhead, Minnesota. The yield was a modest 193 kg PLS (Pure Live Seed) or 13.6 kg/ha, but this first time cost of $7.01/kg PLS was less than half the cost of commercial varieties. Because there were still large tracts of

TABLE 1. Harvest site summary.

	Year	District	Total Yield Kilograms	Area Harvested Hectares	Yield kg/ha	Cost($)/ Kilogram PLS
North Dakota	81	Valley City WMD	68	14.2	4.8	--
	81	Tewaukon NWR	181	6.1	29.6	--
	82	Valley City WMD	227	6.5	34.7	--
	83	Tewaukon NWR	91	4.0	22.4	--
			567	30.8	$\bar{x}$ 18.4	
Minnesota	79	Detroit Lakes WMD	193	14.2	13.6	7.01
	80	Detroit Lakes WMD	1,227	147.3	8.3	5.27
	80	Big Stone NWR	191	8.1	23.5	4.96
	81	Detroit Lakes & Fergus Falls WMDs	2,172	283.3	7.6	6.88
	82	Litchfield WMD	67	4.0	16.5	15.87
	82	Detroit Lakes WMD	814	117.4	6.9	6.61
	82	Fergus Falls WMD	1,997	97.1	20.6	3.11
	83	Detroit lakes WMD	837	67.2	12.4	4.74
	83	Fergus Falls WMD	1,663	93.5	17.8	4.10
	83	Big Stone NWR & Morris WMD	1,465	66.8	21.9	3.70
			10,626	898.9	$\bar{x}$ 11.8	$\bar{x}$ 4.94
MN & ND		Grand Total	11,193	929.7	$\bar{x}$ 12.0	

WMD = Wetland Management District NWR = National Wildlife Refuge
PLS = Pure Live Seed

TABLE 2. Native species that have exceeded 1% in harvest mixes in approximate order of dominance.

Scientific Name	Common Name
Andropogon gerardi Vitman.	Big bluestem
Sorghastrum nutans (L.) Nash.	Indiangrass
Schizachyrium scoparium (Michx.) Nash.	Little bluestem
Sporobolus heterolepis Gray.	Prairie dropseed
Sporobolus asper (Michx.) Kunth.	Tall dropseed
Panicum virgatum L.	Switchgrass
Agropyron trachycaulum (link.) Stendl. var. trachycaulum and var. unilaterale(Cassidy.)	Slender and bearded wheatgrass
Liatris pycnostachya Michx. L. aspera L. Michx. and ligulistylis (A. Nels.) K. Schum.	Blazing star
Helianthus maximiliani Shrader.	Maximillian sunflower
Thalictrum dasycarpum Fisch. & Ave. Lall.	Tall meadowrue
Petalostemum purpureum (Vent.) Rydb.	Purple prairie clover

TABLE 3. Additional species identified in seed analysis - never exceeding one percent of total mixture (listed in alphabetical order).

Scientific Name	Common Name
Agrostis hyemalis (Walt.) BSP.	Hairgrass
Agropyron smithii Rydb.	Western wheatgrass
Amorpha canescens Pursh.	Leadplant
Aster spp.	Asters
Bouteloua curtipendula (Michx.) Torr.	Sideoats grama
Bouteloua gracilis (HBK.) Lag.	Blue grama
Bromus kalmii Gray.	Kalm's brome
Calamagrostis canadensis (Michx.) Beauv.	Bluejoint
Carex spp.	Sedge
Cirsium flodmanii (Rydb.) Arthur.	Prairie thistle
Elymus candensis L.	Canada wildrye
Galium boreale L.	Bedstraw
Helianthus spp.	Wild sunflower
Heliopsis helianthoides (L.) Sweet.	Rough ox-eye
Hieracium spp.	Hawkweed
Juncus tenuis Wild.	Path rush
Monarda fistulosa L.	Monarda
Oenothera biennis L.	Evening primrose
Pycnanthemum virginianum (L.) Durand & Jackson.	Mountain mint
Ratibida columnifera (Nutt.) West.& Standl.	Prairie coneflower
Sisyrinchium spp.	Blue-eyed grass
Solidago canadensis L.	Canada goldenrod
Solidago rigida L.	Rigid goldenrod
Spartina pectinata Link.	Big cordgrass
Verbena spp.	Wild verbena
Zizia spp.	Golden Alexanders

TABLE 4. Total 1983 prairie harvest - Fergus Falls Wetland Management District (Harvest from three sites).

Common Name	Yield in Kilograms PLS (Pure Live Seed)
Big bluestem	978.3
Little bluestem	196.8
Indiangrass	247.6
Prairie dropseed	154.6
Tall dropseed	48.0
Switchgrass	7.8
Tall meadowrue	14.2
Blazing star	16.4
Total	1,663.9
Other crop*:	77.8 kg bulk

*Blazing star, goldenrod, Maximillian sunflower, big cordgrass, switchgrass, bearded wheatgrass, meadowrue, milkweed, leadplant (probably purple prairie clover), crested wheatgrass (?), bluegrass, sedge, wild sunflower, red clover.

Total bulk weight: 3,293 kg

native prairie left in the area under FWS, TNC and State of Minnesota ownership, the possibility of using these tracts for a seed source appeared feasible.

Other FWS stations in Minnesota and North Dakota were soon to follow with harvest and the process was gradually perfected resulting in a 1983 total harvest of 3,966 kg PLS. Through the 1983 harvest, 10,626 kg PLS were harvested from 898.8 ha of native prairie in Minnesota. Average yield was 11.8 kg/ha with a range from 6.9 - 23.5 kg/ha. Average cost (includes all labor and miscellaneous costs) was $4.94/kg PLS with a range from $3.11 - $15.87/kg PLS. An additional 567 kg PLS were harvested from 30.8 ha of native prairie in North Dakota. Average yield was 18.4 kg/ha with a range from 4.8 - 34.7 kg/ha. Cost values were not determined.

Overall yields were much lower than could be obtained from a monoculture. Big bluestem yields in excess of 100 kg/ha are not uncommon on irrigated monocultures. Cost, however, was far below the commercial cost of $14/kg PLS (Table 1).

State seed laboratories have so far discovered 37 native species in the mixture. Eleven species have at times represented at least one percent (purity) of an individual harvest (Table 2). Big bluestem has nearly always been the dominant species. The percentage of Indiangrass has exceeded big bluestem in two lots. The other nine species generally do not exceed ten percent of the mixture.

Twenty-six of the species never exceeded one percent of an individual harvest (Table 3). There are, no doubt, more species occurring in the mixture. The species are reported from the seed laboratories in common names and in some cases a common name probably represents more than one species. Also, there are probably less common species occurring in the mixture that are not

TABLE 5. Analysis for Lot 83-1 Ottertail Prairie.

Common Name	% Purity	% Germination	% Dormant	% Pure Live Seed
Big bluestem	36.65	88	1	36.62
Little bluestem	13.48	74	4	10.51
Indiangrass	14.19	88	0	12.49
Prairie dropseed	1.02	44	20	.65
Tall dropseed	4.75	40	0	1.90
				58.17

Other crop: 3.57% bulk

*Blazing star, goldenrod, Maximillian sunflower, big cordgrass, switchgrass, bearded wheatgrass, meadowrue, crested wheatgrass (?), milkweed.

Inert: 26.34% bulk
Weed Seed: none

discovered in a small sample. Table 4 represents a fairly typical composition of a total annual harvest from an individual.

Germination plus dormant values compare well with commercial origin seed. These values for the major grass species generally are between 65 and 80 percent. Germination for big bluestem has never been less than 50 percent. Generally, percent PLS after cleaning is approximately 50 percent. Table 5 gives an example of one of the lots with excellent germination.

CONCLUSIONS

Through the 1983 harvest, 11,193 kilograms PLS of a prairie seed mixture were harvested from native tall grass prairies in Minnesota and North Dakota. Yields were substantially lower than commercial growers obtain from monocultures, but total cost to the FWS was approximately one-third the commercial cost. Even though yields are low, enough native tall grass prairie occurs in our area to harvest the quantities needed to maintain an active seeding program for nesting cover purposes. Contrary to what the SCS experienced in earlier years, prairie harvest appears to provide a reliable source even in drier years. This may be explained by many of our harvest areas being naturally sub-irrigated or SCS may have harvested in areas of lesser precipitation. Also yields in northwestern Minnesota may be increased due to the compressed nature of the growing season. The target species mature closely enough together to harvest at the same time, whereas in a more southern latitude, fewer of the target species would be mature at any one time.

Quality and composition of the seed appears more than adequate. However, the most important benefit of the harvest has been obtaining locally adapted seed with a greater diversity than can be obtained commercially.

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THE PERFORMANCE OF SELECTED CULTIVARS OF WARM SEASON GRASSES IN THE NORTHERN PRAIRIE AND PLAINS STATES

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Abstract. Plant performance is reported on four warm season grass evaluation plantings seeded from 1982-1984 near Fergus Falls, MN, [Major Land Resource Area (MLRA) 102A; USDA-SCS 1981]; Upham, ND (MLRA 55A); Lake Andes, SD (MLRA 55C); and Pierre, SD (MLRA 53C). Seed origin ranged from North Dakota to Oklahoma. Plant stands during year of establishment were rated good to excellent at all four sites. The effect of seed source on performance and survival was apparent. On the North Dakota site, winter injury was documented for most cultivars originating from central Nebraska and southward. No injury was noted on the switchgrass cultivars, regardless of origin. When winter injury did not occur, southern cultivars generally had higher forage production. Plant density was generally higher for the northern origin cultivars. Northern cultivars moved more than 200 miles southward of their origin generally perform poorly. Forage yield was significantly less than local or more southern cultivars. Plant phenology varied among cultivars and among sites.

INTRODUCTION

Increased interest in the warm season prairie grasses for pasture management, range seeding, erosion control, and wildlife habitat has created the need for additional information on plant performance and area of adaptation. Warm season grasses are recognized as important forage producers in the southern and central plains states, but have been used to only a limited extent in the northern plains. Spring and fall temperatures in this region are ideal for cool season species, but during the summer months, warm season grasses have increased growth and higher forage quality. Livestock producers recognize higher livestock gains when using warm season grasses during summer months (Anderson et al. 1985, Gates 1982, Ross and Kruger 1976). Erosion control and wildlife benefits are compatible when using warm season species (Duebbert et al. 1981, Thornburg 1982). Cool season species can be controlled early in the year with glyphosate, and atrazine can be used effectively for foxtail (*Setaria* sp.) control on certain species (Martin et al. 1981). Improved grass drills, higher seed quality, and closer attention to seedbed preparation have also improved stand establishment (Gunderson 1985). Burning may be used as a management tool to increase stand vigor, seed production, and reduce weed competition (Aldous 1934, Anderson et al. 1970, Kirsch and Kruse 1972).

Natural distribution of a species is based on ecological principles that compensate for a diversity of environments. Ecotypes evolve which are best adapted to the local climate, soil and daylength. When artificially transferred, performance and longevity is uncertain. Generally, southern cultivars mature too late in northern latitudes to produce viable seed. Vigorous growth into late fall increases their susceptibility to winter injury (Rogler 1943). Although increased forage yields may result, loss of stand and lack of seed for stand perpetuation are negative impacts (Warnes et al. 1971). Temperature and photoperiod requirements are extremely variable, particularly within geographical strains of grasses. Disease problems and low yields are generally associated

TABLE 1. Evaluation site information.

Site	Seeding Date	Soils	Avg.Annual Precip.	Moisture Conditions 1982	1983	1984	1985	Establishment
Fergus Falls, MN	June 7-9, 1982	Barnes and Langhei loam	19 to 24 inches (48.3-61 cm)	good	good	good	exc.	excellent
Upham, ND	June 14-16, 1982	Great Bend silty clay loam	15 to 18 inches (38.1 to 45.7 cm)	good	good	poor	good	excellent
Lake Andes, SD	June 7-8, 1983	Agar silt loam	17 to 21 inches (43.2 to 53.3 cm)	-	good	exc.	fair	very good
Pierre, SD	May 23-24, 1984	Lowry silt loam	17 to 19 inches (43.2 to 48.3 cm)	-	-	exc.	poor	excellent

with northern cultivars of grasses that are grown further south, where summer days are shorter (Newell 1968).

The effect of strain source or seed origin is recognized as an important factor in plant performance. Newell (1968) noted that for purposes of varietal improvement of prairie grasses as forage and conservation crops, opportunities still exist for the collection of superior strains that have evolved within a particular environment. Cooper (1957) reported that the area of full adaptation of native cultivars may be relatively narrow. When moved out of the area of full adaptation they respond much as exotics and for that reason cannot be considered permanent. Recognizing this inherent variability within individual populations and/or cultivars of a species is essential to establishing permanent vegetative cover.

For several decades, selection programs have been initiated to develop new and better cultivars of warm season grasses. Numerous differences in seedling characteristics, leaf texture, leafiness, height, forage yield, forage quality, and phenology have been recognized (McMillan 1959, Nielson 1944, Olmstead 1944, Rogler 1943). Cornelius (1947) found a high correlation between early flowering and low dry weight. Individual clones of little bluestem were found to respond differently to different photoperiods based on plant origin (Larsen 1947).

With increased planting of warm season grasses for conservation and production purposes, more information is needed on plant performance and areas of adaptation. Documentation on stand establishment, winter injury, forage yield, phenology, and longevity

TABLE 2. Average annual forage production (lb/ac), oven-dried, at Fergus Falls, Upham, Lake Andes, and Pierre field evaluation planting sites.

	Fergus Falls, MN				Upham, ND				Lake Andes, SD			Pierre, SD
	1983	1984	1985	$\bar{x}$	1983	1984	1985	$\bar{x}$	1984	1985	$\bar{x}$	1985
Big Bluestem												
NDG-4 (ND) 1/	4139^{A} 2/	3283^{B}	2615^{A}	3346	6270^{AB}	6181^{A}	5298^{A}	5916	2372^{C}	4907^{A}	3590	405^{C}
SD-27 (SD)	5058^{A}	4370^{AB}	3981^{A}	4470	6471^{AB}	3444^{C}	4486^{A}	4800	4086^{ABC}	2441^{A}	3264	666^{BC}
SD-43 (SD)	4613^{A}	6623^{A}	3908^{A}	5048	7981^{A}	6361^{A}	6269A	6870	4887^{A}	4262^{A}	4575	889^{BC}
Champ (NE)	3875^{A}	4813^{AB}	4664^{A}	4451	6719^{AB}	4695^{B}	4347^{A}	5254	4114^{ABC}	4164^{A}	4139	1148^{ABC}
Pawnee (NE)	5295^{A}	5591^{AB}	4059^{A}	4982	5877^{AB}	5075^{AB}	4641^{A}	5198	3658^{ABC}	4084^{A}	3871	1545^{AB}
Kaw (KS)	4673^{A}	3892^{AB}	3108^{A}	3891	4601^{AB}	5194^{AB}	6189^{A}	5328	5629^{A}	3846^{A}	4738	1988^{A}
Rountree (IA)	----------Not Planted----------				----------Not Planted----------				3426^{BC}	3663^{A}	3545	1167^{ABC}
Sand Bluestem												
Goldstrike (NE)	2673^{A}	5247^{A}	2780^{A}	3567	6234^{A}	5922^{A}	3357^{B}	5188	2702^{A}	3996^{A}	3349	1132^{A}
Garden (NE)	3076^{A}	3672^{A}	3832^{A}	3527	7855^{A}	3705^{B}	7266^{A}	6275	3073^{A}	4134^{A}	3604	1567^{A}
Indiangrass												
ND-444 (ND-SD)	4566^{AB}	3852^{A}	2234^{A}	3551	4918^{A}	2419^{AB}	4410^{A}	3916	2890^{B}	2413^{B}	2652	365^{A}
Holt (NE)	5428^{A}	5791^{A}	4562^{A}	5260	4330^{A}	3190^{A}	4219^{A}	3913	3412^{B}	4021^{AB}	3717	1014^{A}
Oto (KS-NE)	4623^{AB}	3041^{A}	2079^{A}	3248	1695^{B}	1750^{B}	3178^{AB}	2208	8098^{A}	5828^{A}	6963	1353^{A}
Osage (KS-OK)	3834^{AB}	5262^{A}	3300^{A}	4132	716^{B}	1736^{B}	3610^{A}	2021	7097^{A}	6382^{A}	6740	869^{A}
Rumsey (IL)	1993^{A}	3570^{A}	3844^{A}	3136	538^{B}	588^{C}	1989^{B}	1038	3612^{B}	3813^{AB}	3713	224^{A}
Prairie Sandreed												
ND-95 (ND)	2446^{A}	3786^{A}	2169^{A}	2800	3437^{A}	3339^{A}	8352^{A}	5043	2000^{A}	536^{A}	1268	1181^{A}
Goshen (WY)	1635^{A}	3376^{A}	3221^{A}	2744	3626^{A}	4522^{A}	7285^{B}	5144	446^{B}	0^{A}	223	1529^{A}

1/ Indicates origin of cultivar.

2/ Duncan's New Multiple Range Test, means with the same letter for each species, location and year, are not significantly different (P=.05).

is essential in determining acceptable qualities and characteristics of a warm season ecotype or cultivar planted for a specific purpose.

In this study, 33 cultivars of 7 species and 2 local mixtures of native, warm season grasses were evaluated at four sites. The plantings are located in different Major Land Resource Areas in North Dakota, South Dakota, and Minnesota. They are being evaluated for pasture planting, range seeding, wildlife habitat and other conservation uses. Entries included all commercially available cultivars and selections in advanced stages of testing and developed for use in the central and northern plains. The entries were big bluestem (*Andropogon gerardii* Vitman), sand bluestem [*Andropogon gerardii* var. *paucipilus* (Nash) Fern], indiangrass [*Sorghastrum nutans* (L.) Nash], switchgrass (*Panicum virgatum* L.), prairie sandreed [*Calamovilfa longifolia* (Hook.) Scribn.], little bluestem [*Schizachyrium scoparium* (Michx.) Nash], and sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.].

EVALUATION SITES

The field evaluation planting sites near Fergus Falls, MN, and Upham, ND, were seeded June 7-16, 1982. The site near Lake Andes, SD was seeded June 7-8, 1983, and the site near Pierre, SD was planted May 23-24, 1984. The soils (Table 1) are similar on all sites. Average annual precipitation varied from a low of 15 to 18 inches (38.1 to 45.7 cm) at Upham, to 19 to 24 inches (48.3 to 61 cm) at Fergus Falls. Annual rainfall varied greatly during the study period and had a significant influence on forage production. Extremely droughty conditions existed at Upham in 1984, and at the Pierre site in 1985. Establishment was very good at the Lake Andes site and excellent on the other three sites.

The Upham site is located near the Canadian border with an average freeze-free period of 100 to 120 days and an average annual temperature of 3° to 4° C. The location is 101° west longitude and 49° north latitude. The Fergus Falls site is in west-central Minnesota, 96° west longitude and 46° north latitude. The average freeze-free period is 120 to 140 days with an average annual temperature of 6° to 9° C. The Pierre site is located in central South Dakota, 101° west longitude and 45° north latitude. The average annual temperature is 7° to 9° C with an average freeze-free period of 130 to 150 days. The Lake Andes site is the most southern planting, near the Nebraska border. The location is 99° west longitude, 43° north latitude. The annual growing season averages 130 to 155 days with an average annual temperature of 7° to 9° C.

METHODS AND MATERIALS

The experimental design of all four plantings is a randomized complete block with three replications for data collection. An evaluation array was also seeded for demonstration purposes. Plot

Table 2: (Continued)

	Fergus Falls, MN				Upham, ND				Lake Andes, SD			Pierre, SD
	1983	1984	1985	$\bar{x}$	1983	1984	1985	$\bar{x}$	1984	1985	$\bar{x}$	1985
Switchgrass												
NDG-965-98 (ND)	3365^{B}	3798^{B}	2277^{C}	3147	6498^{D}	5164^{B}	4534^{B}	5399	3141^{C}	4329^{B}	3735	1154^{D}
Sunburst (SD)	6240^{AB}	9113^{A}	7016^{AB}	7456	9639^{A}	7635^{A}	7581^{A}	8285	5808^{AB}	6318^{AB}	6063	3560^{ABC}
SD-149 (SD)	5909^{AB}	4292^{B}	3901^{BC}	4701	8037^{BC}	6356^{AB}	6475^{AB}	6956	5373^{B}	6433^{AB}	5903	3083^{BC}
Neb-28 (NE)	3412^{B}	6104^{AB}	3635^{BC}	4384	6859^{CD}	7428^{AB}	7167^{AB}	7151	5854^{AB}	5948^{AB}	5901	2217^{CD}
Summer (NE)	9011^{A}	7286^{AB}	7564^{A}	7954	9426^{AB}	5410^{AB}	6717^{AB}	7184	6376^{AB}	7285^{A}	6831	3882^{AB}
Pathfinder (NE)	9551^{A}	7078^{AB}	4827^{ABC}	7152	8782^{AB}	6867^{AB}	6940^{AB}	7530	7102^{A}	6945^{A}	7024	5076^{A}
Cave-in-Rock (IL)	4910^{B}	5916^{AB}	4579^{ABC}	5135	6900^{CD}	5298^{AB}	5857^{AB}	6024	5144^{B}	7291^{A}	6218	3053^{BC}
Blackwell (OK)	7152^{AB}	8613^{A}	5066^{ABC}	6944	9335^{AB}	5911^{AB}	7493^{AB}	7580	6664^{AB}	7411^{A}	7038	4674^{A}
Sideoats Grama												
Killdeer (ND)	1372^{A}	1189^{AB}	685^{B}	1082	5354^{A}	3844^{A}	4472^{A}	4557	3559^{A}	2776^{A}	3168	333^{B}
Pierre (SD)	1789^{A}	1189^{AB}	914^{B}	1297	4432^{A}	3475^{AB}	4303^{A}	4070	3572^{A}	2921^{A}	3247	388^{B}
Trailway (NE)	1795^{A}	2683^{A}	1911^{A}	2130	3529^{A}	2542^{B}	2965^{B}	3012	4602^{A}	3865^{A}	4234	1189^{B}
Butte (NE)	1782^{A}	947^{B}	835^{B}	1188	5427^{A}	3978^{A}	4315^{A}	4573	3827^{A}	3069^{A}	3448	2184^{A}
Little Bluestem												
Blaze (NE)	2010^{A}	4146^{A}	2635^{AB}	2930	3123^{AB}	2975^{AB}	3701^{B}	3266	2634^{A}	1617^{B}	2126	1617^{A}
Camper (NE)	3978^{A}	3211^{A}	2229^{B}	3139	3915^{A}	3421^{A}	4773^{A}	4036	3747^{A}	4014^{AB}	3881	648^{A}
Aldous (KS)	3036^{A}	4747^{A}	5299^{A}	4361	1215^{B}	2307^{AB}	2978^{C}	2167	3753^{A}	4284^{A}	4019	1037^{A}
Cimarron (KS-CO-NM-OK)	2766^{A}	3836^{A}	4654^{AB}	3752	1330^{B}	1586^{B}	4061^{B}	2326	3732^{A}	4185^{A}	3959	2483^{A}
Native Mix 1/												
ND-3784 (MN)	2293^{A}	2248^{A}	2361^{A}	2301	5132^{A}	4163^{A}	5145^{A}	4813	-----Not Planted------			Not Planted
ND-3785 (MN)	2824^{A}	3658^{A}	2197^{A}	2893	5437^{A}	4336^{A}	4041^{A}	4605	-----Not Planted------			Not Planted

1/ Native harvest from Minnesota, predominantly big bluestem, some indiangrass.

size varied: 12 by 85 feet (3.7 by 25.9 m) at Fergus Falls; 15 by 100 feet (4.6 by 30.5 m) at Upham; 12 by 60 feet (3.7 by 18.3 m) at Lake Andes; and, 15 by 100 feet (4.6 by 30.5 m) at the Pierre site. Seeding rates were 80 PLS/ft² (860 PLS/m²). A clean, firm seedbed was prepared at all four sites by disking, harrowing and roller packing. The plots were seeded with a grass drill equipped with seedbox agitators, packer wheels, double disk furrow openers, 3/4 inch (1.9 cm) depth bands, and 8 inch (20.3 cm) row spacing. After establishment, 2,4-D was applied for broadleaf weed control and glyphosate was used for spot treatment of persistent perennials. Atrazine was used primarily for foxtail (*Setaria* sp.) control. Spring burning was used as part of the management plan at Fergus Falls and Upham. The plots were mowed early in the year at Lake Andes and Pierre, and the residue removed.

Data collected have included stand ratings, plant height, weed contamination, plant index density, phenology and annual forage production. Plant density (Table 3) was determined by estimating the number of plants in a 9 by 16 inch (22.9 by 40.6 cm) quadrat [1.0 ft² (0.093 m²)]. Ten quadrats were systematically counted near the center of each plot. Estimates were used rather than actual counts because the high plant population on some plots made the determination of individual plants difficult. An index that ranged

TABLE 3. Average index density (plants/ft²) at Fergus Falls, Upham, Lake Andes, and Pierre field evaluation planting sites.

	Fergus Falls, MN			Upham, ND				Lake Andes, SD	Pierre, SD		
	1983	1984	$\bar{x}$	1982	1983	1984	$\bar{x}$	1984	1984	1985	$\bar{x}$
Big Bluestem											
NDG-4	18	28	23	22	33	34	30	27	21	34	28
SD-27	19	31	25	27	33	36	32	39	22	30	26
SD-43	18	22	20	22	26	27	25	24	21	30	26
Champ	9	19	14	21	19	23	21	15	19	31	25
Pawnee	13	28	21	22	25	30	26	29	26	35	31
Kaw	17	25	21	21	13	19	18	29	18	31	25
Rountree	- Not Planted -			-	Not Planted		-	16	15	26	21
Sand Bluestem											
Goldstrike	10	22	16	24	28	33	28	16	29	34	32
Garden	12	26	19	22	28	34	28	15	20	36	28
Indiangrass											
ND-444	17	29	23	16	18	19	18	16	14	25	20
Holt	11	23	17	16	14	26	19	15	24	29	27
Oto	17	25	21	18	5	7	10	20	21	24	23
Osage	10	21	16	16	3	5	8	22	17	21	19
Rumsey	3	9	6	13	3	8	8	2	14	3	9
Prairie Sandreed											
ND-95	8	21	15	9	9	19	12	18	10	21	16
Goshen	6	17	12	5	9	16	10	5	7	18	13
Switchgrass											
NDG-965-98	23	29	26	24	30	32	29	29	21	32	27
Sunburst	17	22	20	15	18	20	18	20	20	37	29
SD-149	23	30	27	20	31	30	27	34	21	35	28
Neb-28	12	20	16	8	8	19	12	28	26	36	31
Summer	17	26	22	24	32	31	29	27	10	31	21
Pathfinder	14	22	18	23	27	30	27	33	18	35	27
Cave-in-Rock	18	18	18	22	15	19	19	20	19	23	21
Blackwell	23	23	23	20	18	21	20	28	20	30	25
Sideoats Grama											
Killeer	24	31	28	20	25	29	25	38	11	21	16
Pierre	24	28	26	19	23	27	23	26	15	30	23
Trailway	10	14	12	16	12	15	14	17	9	20	15
Butte	22	26	24	21	23	28	24	26	10	21	16
Little Bluestem											
Blaze	9	23	16	20	19	29	23	18	12	26	19
Camper	13	26	20	19	21	29	23	26	11	28	20
Aldous	6	15	11	15	5	16	12	17	14	22	18
Cimarron	6	16	11	22	6	16	15	26	11	22	17
Native Mix 1/											
ND-3784	19	25	22	22	30	34	29	- Not Planted -	- Not Planted -		
ND-3785	17	29	23	18	21	30	23	- Not Planted -	- Not Planted -		

1/ Native harvest from Minnesota, predominantly big bluestem, some indiangrass.

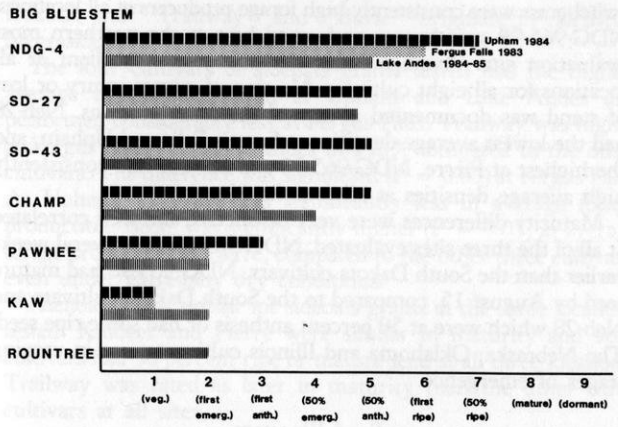

FIG. 1. Average stage of maturity for big bluestem through the growing season (Aug. 15) at Upham, Fergus Falls, and Lake Andes field evaluation planting sites.

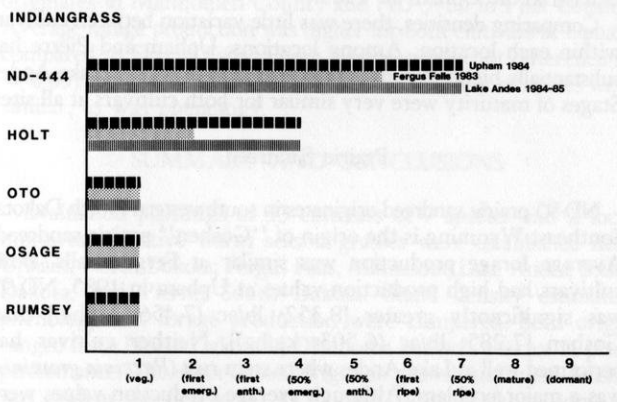

FIG. 2. Average stage of maturity for indiangrass through the growing season (Aug. 15) at Upham, Fergus Falls, and Lake Andes field evaluation planting sites.

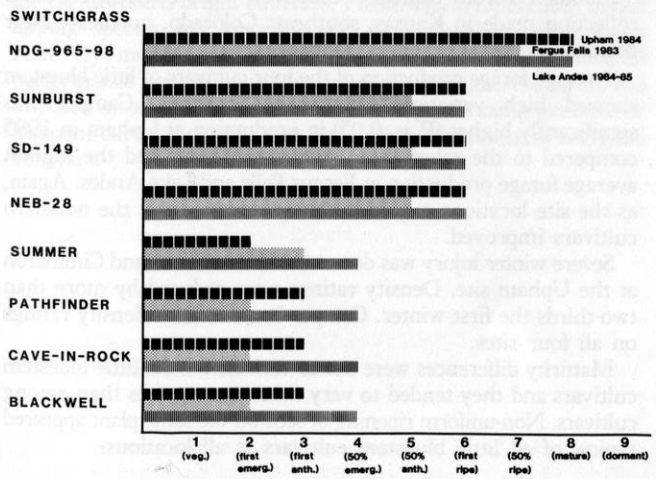

FIG. 3. Average stage of maturity for switchgrass through the growing season (Aug. 15) at Upham, Fergus Falls, and Lake Andes field evaluation planting sites.

from 0 to 40 plants per square foot (0 to 431 plants/m²) was used for each subsample. Oven-dry forage production has been sampled at all sites beginning the second year following establishment. Forage production (Table 2) was determined by clipping a 2 by 10 foot (0.61 by 3.05 m) subplot in each plot with a forage harvester. Sampling dates were as close as possible to the end of the growing season. The sample areas were systematically located in the same position within each plot across the treatment and clipped to a stubble height of three inches (7.6 cm). After weighing the large samples, small (100 gm) grab-samples were also weighed, oven-dried at 60° C for 48 hours, and reweighed to determine moisture content. Percent dry matter weight of the large samples was then used to determine average annual forage production.

Phenology data (Figs. 1-5) were collected at Upham in 1984 and Lake Andes in 1984 and 1985. Phenology at Fergus Falls was evaluated in 1983 by Wendell Olson, Range Conservationist with the USDI Fish and Wildlife Service. Because of drought conditions at the Pierre site in 1985, many cultivars did not produce seed stalks, thus the data was not included in this paper.

RESULTS AND DISCUSSION

Table 2 shows average annual forage production values for the four sites. Average index densities are documented in Table 3. Figs. 1-5 document average stages of maturity on August 15. No stress was imposed on any of the plots by grazing pressure or periodic mowing. This should be kept in mind when considering area of adaptation, as any stress may further limit the adaptation of marginal cultivars.

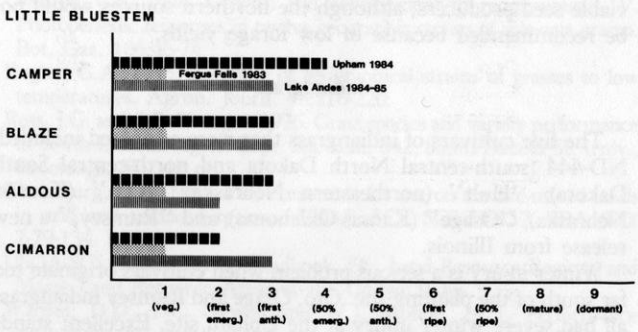

FIG. 4. Average stage of maturity for little bluestem through the growing season (Aug. 15) at Upham, Fergus Falls, and Lake Andes field evaluation planting sites.

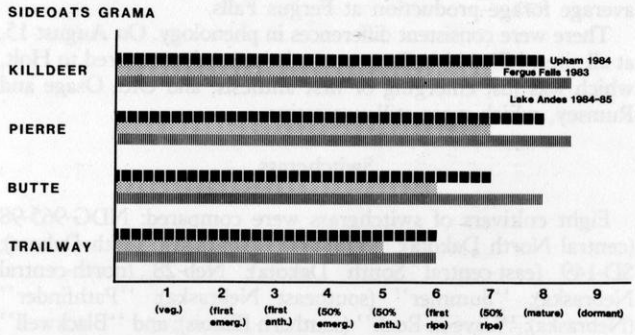

FIG. 5. Average stage of maturity for sideoats grama through the growing season (Aug. 15) at Upham, Fergus Falls, and Lake Andes field evaluation planting sites.

Big Bluestem

The seven cultivars of big bluestem that were evaluated included: NDG-4 (central North Dakota); SD-27 (east-central South Dakota); SD-43 (South Dakota); "Champ" (Nebraska); "Pawnee" (south-central Nebraska); and "Kaw" originating in east-central Kansas . The cultivar "Rountree" (west-central Iowa) was included in the field evaluation plantings at Lake Andes and Pierre.

The highest average forage production for big bluestem has been at the Upham site. SD-43 and NDG-4 over a three year period, averaged 6,870 and 5,916 lb/ac (6,133 and 5,281 kg/ha), respectively. SD-43 also had the highest average forage production at Fergus Falls. At the more southern sites, Lake Andes and Pierre, Kaw (Kansas) has the highest average forage production. Generally, the southern cultivars will have higher forage production if winter injury or drought conditions are not a factor.

Density indexes were generally lower for Champ, Kaw and Rountree, and higher for the more northern cultivars, although good to excellent stands were obtained at all four sites.

The greatest variation among big bluestem cultivars was in phenology. As of August 15 at the Upham site, NDG-4 big bluestem had 50 percent ripe seed, as opposed to Kaw which was still vegetative. The differences were less, as the planting sites moved south. The least variation among cultivars was at the Lake Andes site. Adapted cultivars should be able to produce viable seed within an average growing season to be considered a permanent planting. Average first killing frost dates are about two weeks apart from north to south at Upham, Fergus Falls and Lake Andes. NDG-4 big bluestem should be considered the only adapted cultivar of big bluestem for northern North Dakota. At the Lake Andes site, all seven cultivars may in a given year be viable seed producers, although the northern sources would not be recommended because of low forage yields.

Indiangrass

The five cultivars of indiangrass that were evaluated included: ND-444 (south-central North Dakota and north-central South Dakota); "Holt" (northeastern Nebraska); "Oto" (Kansas-Nebraska); "Osage" (Kansas-Oklahoma); and "Rumsey," a new release from Illinois.

Winter injury is a serious problem when cultivars originate too far south of the planting site. Oto, Osage and Rumsey indiangrass all had severe winter injury at the Upham site. Excellent stands the first year, were gone the second year. Holt, originating from northern Nebraska, had only minor winter injury. ND-444, the only North Dakota cultivar, had no injury. Rumsey had the lowest average stand density at all four locations.

Average forage production varied considerably, again with the more southern cultivars performing best at Lake Andes, and the more northern sources doing better Upham. Holt had the highest average forage production at Fergus Falls.

There were consistent differences in phenology. On August 15, at all sites, ND-444 indiangrass had ripe seed, compared to Holt, which was just emerging or first anthesis, and Oto, Osage and Rumsey, which were still vegetative.

Switchgrass

Eight cultivars of switchgrass were compared: NDG-965-98 (central North Dakota); "Sunburst" (southeast South Dakota); SD-149 (east-central South Dakota); Neb-28 (north-central Nebraska); "Summer" (southeast Nebraska); "Pathfinder" (Nebraska); "Cave-in-Rock" (southern Illinois); and "Blackwell" (north-central Oklahoma).

Average forage production values for the switchgrass cultivars were relatively high at all locations, except for Pierre in 1985 because of drought conditions. The influence of southern origin on increased production was evident. Sunburst and Summer switchgrass were consistently high forage producers at all locations. NDG-965-98 switchgrass performed best at the northern most evaluation site. Average index densities were excellent at all locations for all eight cultivars. No sign of winter injury or loss of stand was documented at any of the four locations. Neb-28 had the lowest average densities at Fergus Falls and Upham, and the highest at Pierre. NDG-965-98 and SD-149 had consistently high average densities at all four locations.

Maturity differences were very distinctive and well correlated at all of the three sites evaluated. NDG-965-98 was several weeks earlier than the South Dakota cultivars. NDG-965-98 had mature seed by August 15, compared to the South Dakota cultivars and Neb-28 which were at 50 percent anthesis or had some ripe seed. The Nebraska, Oklahoma and Illinois cultivars were in varying stages of emergence.

Sand Bluestem

"Goldstrike" and "Garden" sand bluestem both originate in Nebraska. Average forage production was highest at Upham. Garden had higher production than Goldstrike at all four locations in 1985. Garden produced more than twice the forage than Goldstrike at Upham in 1985.

Comparing densities, there was little variation between cultivars within each location. Among locations, Upham and Pierre had substantially higher density ratings than Fergus Falls or Lake Andes. Stages of maturity were very similar for both cultivars at all sites.

Prairie Sandreed

ND-95 prairie sandreed originates in southwestern North Dakota. Southeast Wyoming is the origin of "Goshen" prairie sandreed. Average forage production was similar at Fergus Falls. Both cultivars had high production values at Upham in 1985. ND-95 was significantly greater [8.352^{A} lb/ac (7,456^{A} kg/ha)] than Goshen [7,285^{B} lb/ac (6,503^{B} kg/ha)]. Neither cultivar has performed well at Lake Andes where stem rust (*Puccinia graminis*) was a major problem. Although average production values were higher at Pierre for Goshen in 1985, there was no significant difference. Average densities were higher for ND-95 at all four sites. Maturity dates were similar for both cultivars, with ND-95 slightly earlier than Goshen.

Little Bluestem

"Blaze" and "Camper" little bluestem originate from Nebraska. "Aldous" is from Kansas. "Cimarron" is a composite from a collection made in Kansas, southeast Colorado, northeast New Mexico and the Oklahoma panhandle.

Average forage production of the four cultivars of little bluestem showed high variation among site locations. Camper was significantly higher ($P = 0.05$) in production at Upham in 1985 compared to the other three cultivars. Aldous had the highest average forage production at Fergus Falls and Lake Andes. Again, as the site locations moved north, performance of the northern cultivars improved.

Severe winter injury was documented for Aldous and Cimmaron at the Upham site. Density ratings were reduced by more than two-thirds the first winter. Camper had excellent density ratings on all four sites.

Maturity differences were not as variable for the little bluestem cultivars and they tended to vary more among sites than among cultivars. Non-uniform ripening of seed on the same plant appeared typical of all little bluestem cultivars at all locations.

Sideoats Grama

"Killdeer" sideoats grama originates from western North Dakota and is the most northern source. "Pierre" is from central South

Dakota, and "Trailway" and "Butte" originate in northeast Nebraska.

The four cultivars of sideoats grama tested had the highest average forage production at Upham and Lake Andes and performed considerably less at Fergus Falls. Trailway was higher at Fergus Falls and Lake Andes in 1985, compared to the other cultivars. The difference was significant (P = 0.05) at Fergus Falls. At Upham, Trailway was significantly less in average forage production. Butte was significantly higher (P = 0.05) in average forage production at Pierre, compared to the other three cultivars, even under extremely dry conditions.

Phenology was similar for sideoats grama at the three locations tested. Killdeer and Pierre were similar in maturity and both cultivars had 50 percent ripe or mature seed at all three locations. Trailway was rated as later in maturity than the other three cultivars at all sites.

Native Mix

Two native seed harvests from northwestern Minnesota, composed primarily of big bluestem and lesser amounts of indiangrass, were evaluated at Upham and Fergus Falls. ND-3784 originates in Mahnomen County and ND-3785 in Polk County. Average forage production was higher for both cultivars at Upham compared to Fergus Falls. There was no significant difference (P = 0.05) between cultivars at each location. Density estimates were similar, as was phenology.

SUMMARY AND CONCLUSIONS

Evaluation plantings of 33 cultivars of 7 species and 2 local mixtures of native warm season grasses were established near Upham, North Dakota; Fergus Falls, Minnesota; Lake Andes, South Dakota; and Pierre, South Dakota. Stand density estimates, phenology and forage production were compared. Seed origin ranged from North Dakota to Oklahoma and was a factor in plant performance. The effect of seed origin on growth and stand density was evident the first year. At Upham, North Dakota, some of the southern cultivars that had excellent stand densities the first year (1982) lost half or more of the plant population the second year (1983) due to winter injury. Winter injury was documented for many cultivars originating from central Nebraska and southward. No injury was noted on the switchgrass cultivars. Forage production showed differences among cultivars at each site. Where winter injury was not incurred, southern cultivars generally had higher forage production. Plant density was generally higher for the northern origin cultivars. Phenological differences varied among species and among sites. Area of adaptation appears relatively narrow for many of the cultivars tested. Overall performance is strongly influenced by plant origin. No stress was imposed on any of the evaluation plantings. Grazing pressure or frequent cuttings may further limit the performance of marginal cultivars.

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PHENOLOGY OF SELECTED VARIETIES OF WARM SEASON NATIVE GRASSES

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Abstract. A uniform garden with three replications of 33 varieties of warm season native grass was established by the U.S. Soil Conservation Service at Fergus Falls, Minnesota. The garden was examined twice weekly from late June through early October 1983. Nine different phenology stages from first emergence of the inflorescences (1) through complete dormancy (9) were recorded. The number of days after June 15 that each variety first achieved a phenology stage was then compared. The trend of southern origin varieties to flower later was very apparent. Among the varieties of *Andropogon gerardi* Vitm., there was approximately 50 days difference in phenology between the extremes of the North Dakota origin NDG-4 and the Kansas origin Kaw. The difference among the varieties of *Panicum virgatum* L. was also approximately 50 days between the extremes of the North Dakota origin NDG-965-98 and the Oklahoma origin Blackwell. The extremes in the varieties of *Sorghastrum nutans* (L.) Nash. varied approximately 75 days between the North Dakota origin ND-444 and the Missouri origin MI-5734. Phenology of *Bouteloua curtipendula* (Michx.) Torr. varied approximately 30 days between the extremes of the North Dakota origin Killdeer and the southern Nebraska origin Trailway. Differences among varieties in the other species in the plots were small due to poor north-south origin representation.

INTRODUCTION

Although several studies have been conducted on ecotypic variation of flowering response in warm season native grasses (Cornelius 1947, Larsen 1947, Olmstead 1944, Riegel 1940), the most extensive works are those of McMillan (1956, 1959, 1965a, 1965b). Of these, the 1959 study at Lincoln, Nebraska relates most specifically to the present study. McMillan's study used a uniform garden (Clausen et al. 1940, Cornelius 1947, McMillan 1956, Olmstead 1944, Riegel 1940, Turesson 1922) to minimize variation due to site differences. Clonal samples of several species of warm and cool season grasses were collected from over 40 locations ranging from northern North Dakota to northern Texas on a north-south gradient and from eastern Wyoming to eastern Iowa on an east-west gradient. As was generally noted in other studies, McMillan determined that warm season grass ecotypes from more northern and western areas flowered earlier than those from more southern and eastern areas and that this response was genetically related to photoperiod. Further analysis of McMillan's data by drawing lines of equal first anthesis on his maps of warm season grass species clearly indicates a southwest to northeast geographic pattern for all species tested. For many species the line intervals are relatively regular and a time-distance relationship can be established on a north-south basis. For big bluestem (*Andropogon gerardi* Vitm.) and switchgrass (*Panicum virgatum* L.), the time-distance relationship is one day difference in reaching first anthesis for every 12-14 miles. For Indiangrass (*Sorghastrum nutans* (L.) Nash.) the time-distance relationship was found to be one day for approximately every 9 miles on a north-south gradient. Sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.) was found to have a 30-day difference in reaching first anthesis between west-central North Dakota and northeastern Kansas ecotypes, but the intervals were less consistent and complex patterns existed in South Dakota. Little bluestem (*Schizachyrium scoparium* (Michx.) Nash.) was found to have a 60-day difference in reaching first anthesis between northeastern North Dakota and southeastern Kansas but the patterns were more irregular and were variable for a particular origin. It should be noted that this time-distance relationship applies only when the ecotypes are grown in the same location.

Since the "dust bowl" era of the 1930's, various cultivars of warm season native grasses have been selected or developed for conservation and production uses. The U.S. Soil Conservation Service (SCS) was responsible for development and release of most varieties, but many were developed by various state universities. SCS recognized very early the extreme variation in warm season native grasses and has long recommended that varieties not be moved more than 300 miles north or 200 miles south of its origin (Duebbert et al. 1981). Varieties moved southward beyond 200 miles have low forage production and are susceptible to disease. Varieties moved northward beyond 300 miles produce more forage, but usually will not form seed (Jacobson et al. 1986) and are susceptible to winter injury (Cornelius 1947, Jacobson et al. 1986, Larsen 1947, Olson 1986).

Although much testing had been done on some individual varieties, the full array of cultivars had never been intensively compared in a uniform garden. In 1982 the SCS, Plant Materials Center at Bismarck, North Dakota, in cooperation with the U.S. Fish and Wildlife Service (FWS) established two uniform gardens. One was established near Upham, North Dakota (Section 10, T. 159 N., R. 78 W.). The other was established near Fergus Falls, Minnesota (NE 1/4 NE 1/4, Section 23, T. 132 N., R. 43 W.).

SCS collected information on stand ratings, plant height, weed contamination, plant index density, phenology and annual forage production at both locations (Jacobson et al. 1986). Van Amburg (1986) collected information on non-structural carbohydrate reserves at both locations. The author collected phenology information in 1983 only at the Fergus Falls site. Accordingly, this paper is concerned only with the Fergus Falls garden.

Thirty-one varieties and two native selections of a big bluestem-Indiangrass mixture were established by seeding. The plot design was a randomized complete block with three replications. More specific information on seeding establishment and site description can be found in Jacobson et al. (1986) and Van Amburg (1986).

The varieties and native selections included for comparison were eight of big bluestem, seven of Indiangrass, two of sand bluestem (*Andropogon hallii* Hack.), two of prairie sandreed (*Calamovilfa longifolia* (Hook.) Scribn.), eight of switchgrass, four of little bluestem, and four of side-oats grama. A specific list of the varieties is given in Table 1. The origins of each variety are given on a map in Fig. 1. The varieties are also described in Jacobson et al. (1986).

The soils at the Fergus Falls site are Barnes and Langhei loam. The average annual precipitation is 62.4 cm. The mean annual temperature is 5.7° C. The average number of frost-free days is 135 days. The average date of the first killing frost is September 23. Complete freezing of the seedlings did not occur until mid-October in the establishment year (1982). This probably allowed for survival of the more southern varieties. The first killing frost did not occur until October 14 in the year of sampling (1983). This allowed for sampling the later phenology stages of the more southern varieties.

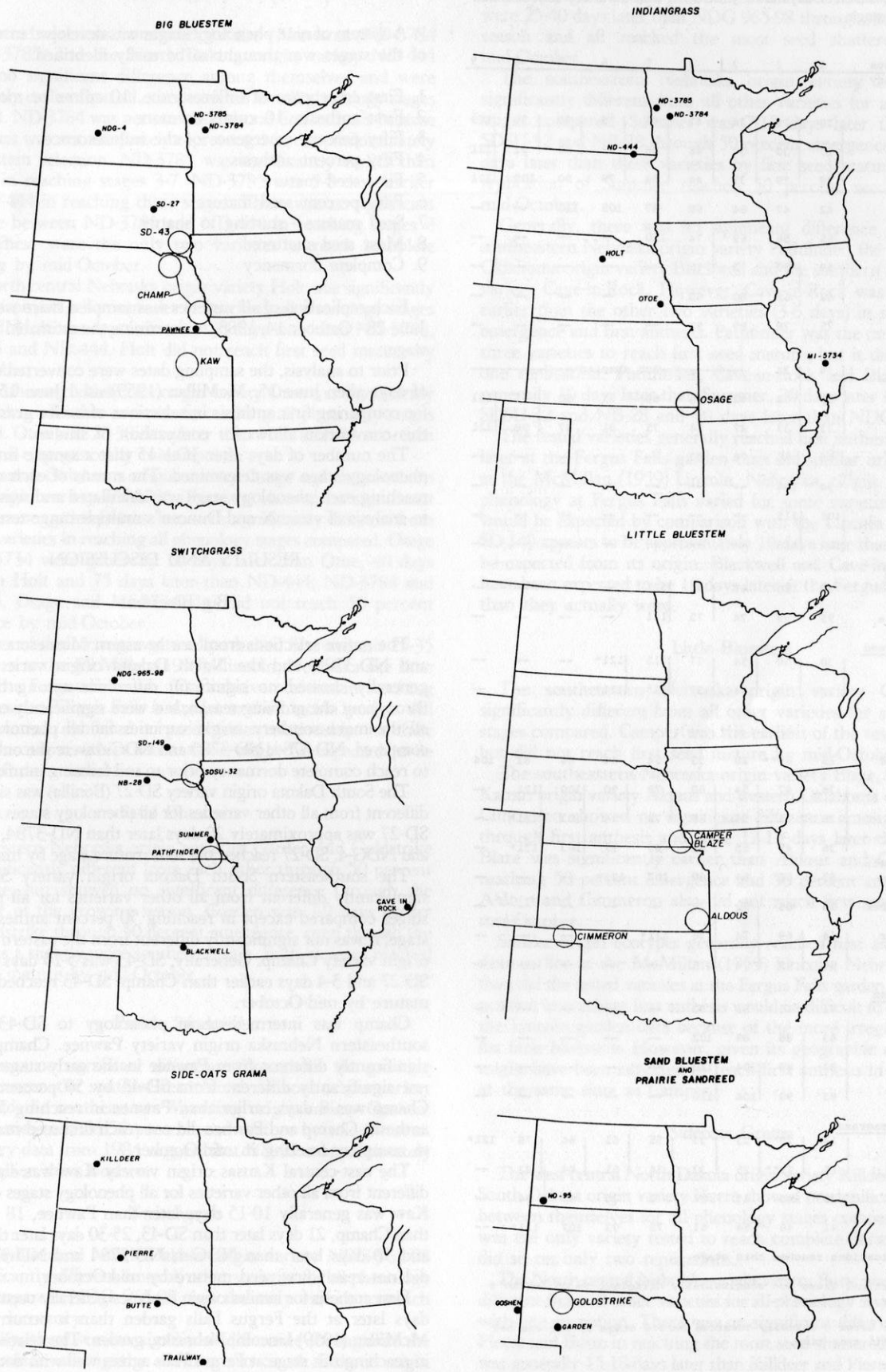

FIG. 1. Origins of selected varieties of warm season native grasses.

TABLE 1. Number of days after June 15th that a variety first reached a phenology stage.

Phenology Stage / Species/Variety	1	2	3	4	5	6	7	8	9
Big Bluestem									
ND-3784	26	29	34	42	66	75	80	90	119
ND-3785	27	30	37	45	66	75	80	91	121
NDG-4	28	29	37	44	64	79	90	105	121
SD-27	42	47	64	69	87	105	115	--	--
SD-43	55	56	69	74	110	--	--	--	--
Champ	59	59	72	75	--	--	--	--	--
Pawnee	62	62	80	83	--	--	--	--	--
Kaw	75	78	89	92	--	--	--	--	--
Indiangrass									
ND-3784	34	34	----------	not sampled	----------				
ND-3785	30	33	42	46	69	75	80	91	121
ND-444	33	33	47	54	75	81	87	98	121
Holt	66	66	78	83	--	--	--	--	--
Otoe	94	104	--	--	--	--	--	--	--
Osage	105	115	--	--	--	--	--	--	--
MI-5734	107	115	--	--	--	--	--	--	--
Sand Bluestem									
Garden	48	50	67	72	121	--	--	--	--
Goldstrike	55	59	74	75	121	--	--	--	--
Prairie Sandreed									
ND-95	30	50	54	57	115	121*	--	--	--
Goshen	29	50	54	57	115	121*	--	--	--
Switchgrass									
NDG 965-98	13	29**	20	33	54	64	69	81	104
SD-149	36	47	54	60	79	90	100	121	--
NB-28	36	47	54	60	78	94	103	121*	--
SDSU-32 (Sunburst)	36	49	55	61	83	97	103	121*	--
Summer	53	56	64	69	107	121*	--	--	--
Cave-in-Rock	58	66	75	76	--	--	--	--	--
Pathfinder	64	69	74	76	121*	--	--	--	--
Blackwell	64	69	74	75	--	--	--	--	--
Little Bluestem									
Camper	71	75	83	83	--	--	--	--	--
Blaze	83	88	89	102	--	--	--	--	--
Aldous	83	89	104	110	--	--	--	--	--
Cimmeron	83	90	104	110	--	--	--	--	--
Side-Oats Gramagrass									
Killdeer	14	29**	23	33	55	61	64	78	121*
Pierre	15	29**	25	33	54	61	64	83	--
Butte	30	40	43	54	70	76	80	94	--
Trailway	41	48	54	61	75	93	107	121*	--

*Not all replications reached this stage.

Connecting vertical lines not statistically different P=.05 Duncan's Multiple Range.

**Investigator error - actually occurred before stage 3, but was not recognized until this time.

METHODS

A system of nine phenology stages was developed in which each of the stages was thought to be easily identified:

1. First emergence of inflorescence, 10 culms or more
2. First anthesis, 10 culms or more
3. Fifty percent emergence of the inflorescences
4. Fifty percent anthesis
5. First seed mature
6. Fifty percent seed mature
7. Seed mature - starting to shatter
8. Most seed shattered
9. Complete dormancy

Each replication of all varieties was sampled twice weekly from June 28 - October 14, 1983, to determine the estimated phenology stage.

Prior to analysis, the sampling dates were converted to number of days after June 15. McMillan (1959) used June 15 as a base for comparing first anthesis in selections of native grasses. Using this convention allows for comparison of studies.

The number of days after June 15 that a sample first reached phenology stage was determined. The means of each variety for reaching each phenology stage was calculated and was subjected to analysis of variance and Duncan's multiple-range test (Table 1).

RESULTS AND DISCUSSION

Big Bluestem

The native selections from northwestern Minnesota (ND-3784 and ND-3785) and the North Dakota origin variety NDG-4 generally showed no significant difference among themselves throughout the growing season, but were significantly earlier than all the more southern origin varieties for all phenology stages compared. ND-3784, ND-3785 and NDG-4 were the only varieties to reach complete dormancy prior to soil freezing in mid-October.

The South Dakota origin variety SD-27 (Bonilla) was significantly different from all other varieties for all phenology stages compared. SD-27 was approximately 20 days later than ND-3784, ND-3785 and NDG-4. SD-27 reached the seed mature stage by mid-October.

The southeastern South Dakota origin variety SD-43 was significantly different from all other varieties for all phenology stages compared except in reaching 50 percent anthesis. In this stage, it was not significantly different from the eastern Nebraska origin variety Champ. Generally, SD-43 was 5-15 days later than SD-27 and 3-4 days earlier than Champ. SD-43 reached first seed mature by mid-October.

Champ was intermediate in phenology to SD-43 and the southeastern Nebraska origin variety Pawnee. Champ was not significantly different from Pawnee in the early stages and was not significantly different from SD-43 by 50 percent anthesis. Champ was 8 days earlier than Pawnee in reaching 50 percent anthesis. Champ and Pawnee did not reach first seed mature prior to complete freezing in mid-October.

The east-central Kansas origin variety Kaw was significantly different from all other varieties for all phenology stages compared. Kaw was generally 10-15 days later than Pawnee, 18 days later than Champ, 21 days later than SD-43, 25-30 days later than SD-27 and 50 days later than NDG-4, ND-3784 and ND-3785. Kaw did not reach first seed mature by mid-October.

First anthesis for similar origin ecotypes generally occurred 10-20 days later at the Fergus Falls garden than it occurred at the McMillan (1959) Lincoln, Nebraska, garden. The relative position in reaching this stage at Fergus Falls agrees well with data obtained from the Lincoln garden. All varieties tested at Fergus Falls exhibited a predictable relationship to their origin in reaching first anthesis.

Indiangrass

The native selections from northwestern Minnesota (ND-3784 and ND-3785) and the North Dakota origin variety ND-444 showed no significant difference among themselves and were significantly earlier than all other varieties for all phenology stages compared. ND-3784 was not sampled beyond first anthesis because Indiangrass was not adequately represented in the predominately big bluestem selection. ND-3785 was significantly earlier than ND-444 in reaching stages 3-7. ND-3785 was 5-8 days earlier than ND-444 in reaching these stages. There was no significant difference between ND-3785 and ND-444 in reaching stages 8 and 9. These were the only two varieties to reach complete dormancy by mid-October.

The north-central Nebraska origin variety Holt was significantly different from all other varieties in reaching all phenology stages compared. Holt was approximately 30 days later than ND-3784, ND-3785 and ND-444. Holt did not reach first seed mature by mid-October.

The southeastern Nebraska origin variety Otoe was significantly different than all other varieties in reaching all phenology stages compared. Otoe was 28-38 days later than Holt and did not reach 50 percent emergence by mid-October.

The Kansas-Oklahoma origin variety Osage and the southern Illinois origin variety MI-5734 (Rumsey) showed no significant difference among themselves, but were significantly different from all other varieties in reaching all phenology stages compared. Osage and MI-5734 were generally 10 days later than Otoe, 40 days later than Holt and 75 days later than ND-444, ND-3784 and ND-3785. Osage and MI-5734 also did not reach 50 percent emergence by mid-October.

Ecotypes of similar origin generally reached first anthesis 25-35 days earlier at the McMillan (1959), Lincoln, Nebraska site than those at the Fergus Falls site. The relative position in reaching first anthesis at Fergus Falls is similar to the Lincoln garden. All varieties tested exhibited a predictable relationship to their geographic origin, except Otoe. Otoe might be expected to be at least 10 days earlier.

Sand Bluestem

The western Nebraska origin varieties Garden and Goldstrike were significantly different from each other through 50 percent emergence, but showed no significant difference through the remainder of the growing season. Garden was 7-9 days earlier than Goldstrike through 50 percent emergence, even though the former has a slightly more southern origin. Both varieties reached first seed mature by mid-October.

Prairie Sandreed

There was no significant difference throughout the growing season between the southwestern North Dakota origin variety ND-95 and the southeastern Wyoming origin variety Goshen. Both varieties reached 50 percent seed mature by mid-October. Preliminary data from 1984 suggest that ND-95 is approximately 6 days earlier than Goshen.

Switchgrass

The south-central North Dakota origin variety NDG-965-98 was significantly different from all other varieties for all phenology stages compared. NDG 965-98 was the only variety to reach complete dormancy.

Generally, there was no significant difference throughout the growing season among the southeastern South Dakota origin varieties SD-149 (Forestburg) and SDSU-32 (Sunburst) and the north-central Nebraska origin variety NB-28. However, SDSU-32 was significantly later (5-6 days) than SD-149 and NB-28 in reaching first seed mature and 50 percent seed mature. These three varieties were 25-40 days later than NDG 965-98 throughout the growing season and all reached the most seed shattered stage by mid-October.

The southeastern Nebraska origin variety Summer was significantly different from all other varieties for all phenology stages compared. Summer was 7-10 days later than SD-149, SDSU-32 and NB-28 through 50 percent emergence, but was 20 days later than these varieties by first seed mature. Only one replication of Summer reached 50 percent seed mature by mid-October.

Generally, there was no siginficant difference between the southeastern Nebraska origin variety Pathfinder, the north-central Oklahoma origin variety Blackwell and the southern Illinois origin variety Cave-in-Rock. However, Cave-in-Rock was significantly earlier than the other two varieties (3-6 days) in reaching first emergence and first anthesis. Pathfinder was the only one of the three varieties to reach first seed mature, but it did so on only one replication. Pathfinder, Cave-in-Rock and Blackwell were generally 10 days later than Summer, 20 days later than SD-149, SDSU-32 and NB-28 and 50 days later than NDG 965-98.

The tested varieties generally reached first anthesis 15-20 days later at the Fergus Falls garden than did similar origin ecotypes at the McMillan (1959) Lincoln, Nebraska, origin. The relative phenology at Fergus Falls varied for some varieties more than would be expected by comparison with the Lincoln garden data. SD-149 appears to be approximately 10 days later than what would be expected from its origin. Blackwell and Cave-in-Rock might have been expected to be 10 days later at the Fergus Falls garden than they actually were.

Little Bluestem

The southeastern Nebraska origin variety Camper was significantly different from all other varieties for all phenology stages compared. Camper was the earliest of the tested varieties, but did not reach first seed mature by mid-October.

The southeastern Nebraska origin variety Blaze, southeastern Kansas origin variety Aldous and western Oklahoma origin variety Cimmeron showed no significant difference among themselves through first anthesis and were 12-15 days later than Camper. Blaze was significantly earlier than Aldous and Cimmeron in reaching 50 percent emergence and 50 percent anthesis. Blaze, Aldous and Cimmeron also did not reach first seed mature by mid-October.

Similar origin ecotypes generally reached first anthesis 25-35 days earlier at the McMillan (1959) Lincoln, Nebraska, garden than did the tested varieties at the Fergus Falls garden. The relative position in reaching first anthesis would be difficult to predict using the Lincoln garden data because of the more irregular patterns for little bluestem. However, given its geographic origin, Blaze might have been expected to reach first anthesis in Fergus Falls at the same time as Camper.

Sideoats Grama

The west-central North Dakota origin variety Killdeer and central South Dakota origin variety Pierre showed no significant difference between themselves for all phenology stages compared. Killdeer was the only variety tested to reach complete dormancy, but it did so on only two replications.

The North-central Nebraska origin variety Butte was significantly different from all other varieties for all phenology stages compared with one exception. There was no significant difference between Pierre and Butte in reaching the most seed shattered stage. Butte was generally 15-18 days later than Killdeer and Pierre throughout most of the growing season.

The southeastern Nebraska origin variety Trailway was significantly different from all other varieties for all phenology

stages compared. Trailway was 5-11 days later than Butte through first seed mature, but the difference between the two widened to more than 20 days in the later stages. Trailway reached the most seed shattered stage on two replications.

First anthesis for similar origin ecotypes generally occurred 10-18 days later at the Fergus Falls garden than it occurred at the McMillan (1959) Lincoln, Nebraska, garden. Because of irregular patterns found by McMillan in side-oats grama, predicting a relationship from his data would be difficult. However, Pierre might be expected to be 7-10 days later than it actually was.

CONCLUSIONS AND RECOMMENDATIONS

The results clearly indicate a latitudinal relationship strikingly similar to that found by McMillan (1959). With a few exceptions, varieties exhibited a predictable relationship to their origin with respect to phenology. Those exceptions in many cases may be explained by variability within a population. Selections that became cultivars in some cases may represent extremes in a population.

Ecotypes of similar origin generally matured 10-30 days later at the Fergus Falls site than did those at Lincoln, Nebraska (McMillan 1959). Most of this can be attributed to temperature differences, but photoperiod differences between the two locations are probably a factor.

The maximum 300 mile northward movement of varieties recommended by SCS appears to be the maximum to where a variety of switchgrass and big bluestem could be reasonably expected to produce seed. Indiangrass is the "last wave" on any tallgrass prairie (McMillan 1959) and probably cannot be expected to form seed at the 300 mile northward movement. Sideoats grams as a species flowers relatively early and could probably be moved farther north than 300 miles for seed production. However, seed formation is just one measure of adaptability and does not necessarily guarantee long term survival. Perhaps a variety may even need to approach complete dormancy to persist long term. Varieties that are in earlier phenological stages at the time of complete freezing may be lower in non-structural carbohydrate crown and root reserves (Van Amburg 1986). Environmental pressures such as a fall wildfire or grazing may be limiting factors.

When considering varieties for planting, the purpose of the planting may dictate choice. If the objective is prairie restoration, it should be remembered that movement of a warm season grass community 300 miles north will result in a community that matures approximately one month later than what occurred naturally in that area. At least aesthetically, the objectives of restoring major components would not be achieved. If the objective is for relatively short term forage production, northward movement approaching the 300 mile limit might be justified.

Intraspecific variation in native warm season grasses with regard to phenology has been found to be extreme and very predictable on a north-south gradient. Because of this, variety choice should assume as great an importance as species choice. If a particular range site or soil type dictates the planting of a particular species and there is no adapted seed source available, perhaps a different species with similar ecological requirements should be considered for use.

A factor that is seldom considered when choosing species and varieties to plant in a mixture is that the various combinations have not been tested as communities but are selected, increased and tested in monocultures. Because it is possible to vary the phenological order of species by choice of varieties, interspecific competition may very well affect even short term survival of some of the components.

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VARIATION IN TOTAL NONSTRUCTURAL CARBOHYDRATE RESERVES IN NATIVE WARM-SEASON GRASS VARIETIES

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Abstract. Adequate carbohydrate reserves are important in perennial plants for winter survival, early spring growth initiation and regrowth initiation after herbage removal. Lower carbohydrate reserves in varieties of southern origin at fall dormancy could result in poor winter survival at northwestern Minnesota latitudes. A study of 31 varieties of seven species of warm season native grasses was designed to determine any significant differences in carbohydrate reserves between varieties within any one species. Plots of the varieties were established by seeding. Plot design was a randomized complete block with three replications. Crowns and roots of each variety from each block were collected after the first frost and analyzed for total nonstructural carbohydrate (TNC) content. Varieties of *Andropogon gerardi, Schizachyrium scoparium* and *Panicum virgatum* did show significant differences in crown and root TNC content. *A. gerardi* varieties originating from more northern latitudes contained greater concentrations of TNC in the crowns and roots at the time of first frost. Varieties of *S. scoparium* and *P. virgatum* showed no clear correlation between latitude and root/crown TNC concentration.

INTRODUCTION

Intraspecific variation is known to be a common phenomenon in literally all living organisms. When this variation is determined to be genetically based, and correlated with habitat, it has been termed ecotypic variation (McMillan 1959). Quinn (1978) has argued that while the concept of genetically-based variation that is habitat correlated is valid, the term "ecotype" should not be used in reference to this concept. Turesson (1922) first introduced the concept of ecotypes. Turesson's basic genecological principles were substantiated by the later work of Clausen et al. (1939, 1940, 1941, 1947, 1948). Extensive studies of ecotypic variation in grasses have been conducted by McMillan (1956, 1959, 1965, 1969). These studies, probably more than any others, have precipitated numerous research efforts directed at ecotypic response (Clary 1979, Heide 1980, Miller 1982, Robertson and Ward 1970, Ward 1969).

The transplant garden, or uniform garden, first introduced by Turesson (1922), has become a standard method for evaluating ecotypic variation (Clausen et al. 1940, Cornelius 1947, McMillan 1956, Olmstead 1944, Riegel 1940). A uniform garden minimizes intraspecific variation due to site differences. Observed differences are then assumed to be genetic.

It has generally been noted that plants from northern and western populations flower earlier than those from southern and eastern populations. Climate selection has resulted in northern communities having populations that can mature under long daylengths and a short frost-free period. More southern communities have populations adapted to shorter daylengths and a longer frost-free period (McMillan 1959). Thus plant material from southern latitudes that is transplanted to more northern sites will likely not be able to mature. Under some conditions, the parent plant may not survive the winter period (Cornelius 1947, Larsen 1947). Winter injury has been reported to occur in northwestern Minnesota warm-season grass plantings established from more southern seed sources (Olson 1986a, Jacobson et al. 1986). Northern populations, when moved southward, flower, set seed and enter dormancy long before the first killing frost. Such plants would certainly be at a competitive disadvantage.

Comparatively little work has been done concerning the differential physiological responses of ecotypes. Hiesey and Milner (1965) have reviewed studies that dealt with physiological response at the ecotype level. Photoperiodism, mineral nutrition and photosynthesis are the responses most studied.

No studies have been conducted to determine possible differences in the levels of carbohydrate reserves between ecotypes of grasses. Adequate carbohydrate reserves are important in perennial plants for winter survival, early spring growth initiation and regrowth initiation after herbage removal (White 1973). Existence of lower carbohydrate reserves in varieties of southern origin at the time of fall dormancy could explain why some southern varieties are winter-killed at northwestern Minnesota latitudes.

This study was designed to determine if significant differences in carbohydrate reserves existed between varieties (ecotypes) of native warm season grasses. The terms variety and ecotype are used interchangeably in this paper. Thirty-one varieties of seven species were studied. The two accessions of native mix (Jacobson et al. 1986) were not included. The seven species were: big bluestem (*Andropogon gerardi* Vitman), little bluestem (*Schizachyrium scoparium* (Michx.) Nash), sand bluestem (*Andropogon hallii* Hack), Indiangrass (*Sorghastrum nutans* (L.) Nash), prairie sandreed (*Calamovilfa longifolia* (Hook) Scribn.), switchgrass (*Panicum virgatum* L.) and sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.). The varieties of these species which were chosen for study are for the most part commercially available varieties. The origins of the varieties are given in Jacobson et al. (1986) and Olson (1986b). These varieties have been used extensively throughout the midwest to establish native grass stands for grazing and wildlife uses. Many times these varieties have been used to establish stands distant from the area of origin and intended use. The success of such plants probably depends in no small part on the degree and type of ecotypic variation within the species.

METHODS AND PROCEDURES

Two uniform plot areas of the 31 varieties were established by seeding (Jacobson et al. 1986). One area was located on the J. Clark Salyer National Wildlife Refuge in northern North Dakota, near Upham (Sec. 10, T159N, R78W). This site is nearly level with a Great Bend Silty Clay Loam soil type. Average annual precipitation is 42.3 cm (16.64 in). The mean annual temperature is 2.8° C (37.0° F). The average frost-free period is 114 days.

A second area was established on the U.S. Fish and Wildlife Service land, adjacent to Fergus Falls, Minnesota (NE 1/4, NE 1/4 Sec. 23, T132N, R43W). This site is approximately 160 mi south and 210 mi east of the Upham, North Dakota site. The topography is gently rolling. Most of the area is mapped as a Barnes Loam soil type, with a small portion of the higher elevation mapped as a Langhei Loam. Average annual precipitation is 62.4 cm (24.56 in). The mean annual temperature is 5.7° C (42.2° F). The average frost-free period is 135 days.

The plots at Fergus Falls, Minnesota were planted June 7-9, 1982. The Upham, North Dakota plots were planted June 14-16, 1982. At both sites the plot design was a randomized complete block with three replications. At Upham, North Dakota each plot was 30.5 m long and 4.6 m wide. At Fergus Falls, Minnesota the plots were 26 m long and 3.7 m wide. Preplant and postplant plot treatment are described by Jacobson et al. (1986).

All plant organs may temporarily store nonstructural carbohydrates. However, the major storage site of carbohydrate reserves in grasses is the lower region of the stem (White 1973). Specifically, the grass crown is considered to be a most important site of carbohydrate storage. The importance of roots as

carbohydrate reserve sites is more questionable. Studies have shown that little carbohydrate reserves of roots are mobilized to the shoots to support regrowth (Davidson and Milthorpe 1966, Marshall and Sagar 1965). It is not known how important the root reserves may be for winter survival. Most studies of carbohydrate reserves in perennial grasses have included both root and crown data. Thus, it seemed prudent to include both roots and crowns as plant components to be analyzed in this study.

Collection of crowns and roots for analysis of total nonstructural carbohydrates (TNC) was undertaken in 1982 only after a killing frost and the grasses had entered winter dormancy. The date of the first killing frost, and thus the sampling date, was different for the two study areas. The Upham, North Dakota site reached a temperature of -2.2° C (28° F) on August 27. Samples were collected on September 17. The growing period for the Upham site, from the planting date of June 16 to the first frost August 27, was 72 days. The Fergus Falls, Minnesota site recorded a temperature of -0.55° C (31° F) on October 16. Samples were collected on November 3. The growing period for the Fergus Falls site (June 9 to October 16) was 129 days.

Roots and crowns of each ecotype within each replicate were sampled. Several plants within each replication were randomly chosen and excavated to a depth of about 15 cm. The leaves and stems were clipped from the crowns and roots and discarded. Soil was removed from the roots and crowns by washing with cold water. The clean samples were immediately frozen with dry ice and held until possible to oven-dry them in the laboratory. Frozen roots and crowns were separated and dried at 100° C for one hour, and at 70° C until completely dry. Dried roots and crowns were ground with a Wiley mill to pass a 40-mesh screen. Ground samples were stored in small, sealed plastic bags until analysis for TNC.

Total nonstructural carbohydrates were extracted from 300 mg samples of the ground roots and crowns. The method of extraction was similar to Smith (1969). However, purified diastase (Fisher Chemical Co.) was used as the enzyme. It was necessary to dialyze the enzyme, using tap water, for a period of four days to remove interfering reducing substances. TNC concentrations within the extracts were determined by a photometric adaptation of the Somogyi method (Nelson 1944), and expressed on a glucose equivalent basis of mg/g plant material.

All data were subjected to analysis of variance, and Duncan's multiple-range test was used to separate ($P < 0.05$) mean differences in TNC content of roots and crowns between the varieties of each species.

RESULTS AND DISCUSSION

At the Upham, North Dakota site varieties of *Andropogon gerardi* and *Schizachyrium scoparium* were found to have significant differences in TNC concentrations in both the roots and crowns (Table 1). The concentration of TNC was consistently higher in the crowns than the roots for all varieties. The *A. gerardi* variety Kaw was an exception, having the root concentration slightly higher than the crown.

Of the *A. gerardi* varieties, NDG-4 had the highest concentration of root and crown TNC (Table 1). Root TNC concentration in variety NDG-4 was significantly greater than the Kaw and the Pawnee varieties. At the 95% level the Duncan's multiple-range test did not show a significant difference between the varieties NDG-4, SD-27, SD-43 or Champ (Table 1). In crown TNC concentration, NDG-4 was significantly greater than the varieties Kaw, Champ or Pawnee. Variety SD-27, having the second highest concentration of TNC in the crowns, was significantly greater than Kaw, but did not differ from the other varieties. The order of the *A. gerardi* varieties, according to TNC concentration, was essentially the same for both the roots and crowns.

Although there were no significant differences shown for the big bluestem varieties grown at the Fergus Falls, Minnesota site, it is interesting to compare that data to data from the Upham, North Dakota site. Roots from the big bluestem plants at Fergus Falls showed little difference in TNC concentration (Table 1). Crowns, on the other hand, exhibited a range of 17 mg/g. In many instances this would be a great enough difference to show significance between means. However, the variation in the data was too large to show such significance. A larger sample size would seem advisable to overcome this. The order of the varieties in TNC concentration in the crowns was very similar at both sites. In both cases the more northern varieties, NDG-4, SD-27 and SD-43 were the highest in TNC concentration.

TABLE 1. Mean TNC concentrations (mg/g) of the roots and crowns of *Andropogon gerardii, Schizachyrium scoparium* and *Panicum virgatum* varieties from the two plot sites. Means not sharing common superscripts within a species, site and sample type are significantly different ($P < 0.05$).

	Upham, ND		Fergus Falls, MN	
	Roots	Crowns	Roots	Crowns
Andropogon gerardi				
Kaw	6.77^{a}	6.56^{a}	50.91	23.01
Pawnee	6.97^{a}	13.04^{ab}	49.50	30.26
Champ	9.26^{ab}	12.81^{ab}	45.46	31.10
SD-43	13.53^{ab}	17.43^{abc}	49.45	39.93
SD-27	13.74^{ab}	23.20^{bc}	51.16	40.01
NDG-4	17.07^{b}	29.67^{c}	52.30	31.30
Schizachyrium scoparium				
Cimmaron	10.85^{a}	15.86^{a}	23.86^{a}	37.51^{a}
Camper	11.10^{a}	21.87^{ab}	20.39^{a}	31.42^{a}
Blaze	15.03^{a}	30.98^{b}	16.68^{a}	28.08^{a}
Aldous	22.55^{b}	33.37^{b}	36.41^{b}	37.90^{a}
Panicum virgatum				
NDG-965-98	28.74^{a}	23.93^{a}	36.39^{a}	30.76^{ab}
Neb-28	31.87^{a}	31.00^{a}	37.29^{ab}	33.19^{ab}
SD-149	24.99^{a}	35.10^{a}	38.50^{ab}	26.52^{ab}
Blackwell	23.43^{a}	25.57^{a}	40.39^{ab}	23.53^{a}
Pathfinder	37.71^{a}	36.12^{a}	44.44^{ab}	39.31^{b}
Sunburst	25.69^{a}	21.83^{a}	44.83^{ab}	29.57^{ab}
Summer	41.48^{a}	37.39^{a}	47.03^{b}	33.05^{ab}
Cave-in-Rock	34.51^{a}	28.03^{a}	61.91^{c}	27.26^{ab}

Root TNC concentration of *Schizachyrium scoparium* variety Aldous was significantly higher than all other little bluestem varieties at the Upham, North Dakota site (Table 1). Aldous was also the variety with the highest crown TNC concentration, but differed significantly only from the variety Cimmaron. The order of the little bluestem varieties, according to TNC concentration, was the same for both the roots and crowns.

Only the roots of the *S. scoparium* varieties at the Fergus Falls, Minnesota site displayed differences in TNC concentration. The roots of Aldous were significantly greater in TNC concentration than the other three varieties. The crown concentration showed the same order of varieties, but no significant differences were found. The data from the two plot sites agree in that the variety Aldous is consistently higher in TNC concentration.

At the Fergus Falls, Minnesota site varieties of *Panicum virgatum* exhibited differences in TNC concentration in the roots and crowns (Table 1). However, the order of the varieties as to TNC concentration, was quite different for the roots and crowns. The Cave-in-Rock variety had a significantly higher concentration of TNC in the roots than any other variety. Of the remaining seven varieties, only Summer was shown to have a root TNC concentration significantly higher than NDG-965-98. Fewer differences were apparent for the TNC concentrations in the *P. virgatum* crowns. Pathfinder crowns were significantly higher than Blackwell in concentration. All other varieties showed no difference.

No differences were found between the *P. virgatum* varieties from the Upham, North Dakota site. However, the range in TNC concentration for both roots and crowns suggests that differences may well exist (Table 1). The order of the varieties in TNC concentration shows little consistency between the two plot sites.

Summer and Pathfinder are generally higher in TNC concentration, while Blackwell is usually at the low end of the range.

The rather large difference in growing season between the two plot sites could have influenced the results. On the average, Fergus Falls, Minnesota has a frost-free period 21 days longer than Upham, North Dakota. During 1982 it had 57 more days being frost-free. This was due to an unusually mild fall in the west-central Minnesota region, and a late date (October 16) for the first frost. This allowed even the varieties of southern origin time to mature. On the other hand, the first frost at Upham, North Dakota was somewhat early (August 27). A number of the varieties at the Upham site were still vigorously growing at the time of the frost.

CONCLUSIONS

The results indicate that there are definite differences in root and crown TNC concentrations between varieties of the same species. At the more northern site near Upham, North Dakota, the varieties of both *A. gerardi* and *S. scoparium* displayed such differences. At the Fergus Falls, Minnesota site the varieties of *P. virgatum* had significant differences in TNC concentration in roots and crowns. *S. scoparium* varieties differed only in TNC concentration in the roots.

For *A. gerardi* varieties there is a clear indication that those of more northern origin contained greater concentrations of TNC in the crowns and roots at the time of first frost. There is no such clear indication for varieties of *P. virgatum* and *S. scoparium*. *S. scoparium* variety Aldous was consistently higher than all other bluestem varieties in both root and crown TNC concentration.

TNC concentration is only one parameter to judge the suitability of a given variety to the environment. Ultimately it is productivity and long-term stand viability that determines the success of a grass variety. It would seem that these factors are related. However, more data must be collected before varietal decisions can be based on carbohydrate reserve differences.

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PRODUCTIVITY POTENTIAL AND CLASSIFICATION OF SELECTED ABANDONED MINE LANDS IN WESTERN NORTH DAKOTA

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Abstract. Abandoned mine lands of western North Dakota resulted from surface mining prior to modern reclamation laws. Of the 616 recognized abandoned mine land sites in North Dakota, spoil materials were collected from different spoil aspects of 35 sites during the summers of 1982 and 1983 to study their properties and productivity potential. *Agropyron smithii* (western wheatgrass) and *Melilotus officinalis* (yellow sweet clover) were grown separately in pots maintained in environmentally controlled growth chambers. The effects of two levels of NPK fertilizer were studied and compared to surface geology, bedrock geology, pH, electrical conductivity (EC), and sodium adsorption ratio (SAR). This produced a preliminary classification of abandoned surface mined lands in North Dakota.

Easily rehabilitated sites, characterized by neutral pH, EC < 4 mmhos, and SAR < 12, are usually located where more than 1.5 m of glacial till overlie Tertiary sediments of the Bullion Creek Formation. Sodic and saline (EC > 8 mmhos, SAR > 12) spoil contains little if any glacial till with sediments from the Sentinel Butte, Slope, and Bullion Creek Formations. Strongly acid sites, those with pH < 4.5, are commonly uraniferous lignite mines in the Sentinel Butte Formation.

Fertilizer had a significant positive effect on the productivity of both species. The highest response was observed in non-toxic materials having unusually low amounts of macronutrients.

INTRODUCTION

Mining for coal has been an ongoing process in western North Dakota since the early part of this century. Before the first reclamation law was implemented in 1970, most of the coal mined lands were abandoned without reclamation (Englerth 1983). The North Dakota Public Service Commission has identified over 600 abandoned mine sites in North Dakota, of which more than 350 were surface mines.

The study, undertaken by Project Reclamation, considers only abandoned surface mined sites, which range in size from less than 0.5 hectare to 730 hectares in size. These mine sites are distributed throughout western North Dakota, with substantial variations in climate, soil parent materials, topography, vegetation, and time since disturbance (Fig. 1). The objectives of this study, supported by the North Dakota Public Service Commission, were to (1) determine the plant species and minespoil properties, (2) delineate edaphic toxicities and environmental stresses limiting plant establishment and growth, and (3) develop a classification of mine sites based upon minespoil diversity and potential productivity as measured under controlled environmental conditions. This paper reports our findings concerning the relationship between potential productivity under controlled conditions and minespoil properties and presents a classification system for abandoned mine lands in North Dakota, which incorporates both geophysical and chemical spoil properties.

MATERIALS AND METHODS

During the summers of 1982 and 1983, thirty-five of the abandoned surface mines, scattered across the western half of North Dakota, were sampled (Fig. 1). Replicated spoil samples were collected at two depths (0-10 cm and 10-30 cm) at each site. This material was air dried, sieved to 2 mm, and equal amounts from each sampling depth were homogenized, after which 400 grams of this homogenized spoil material were placed in each undrained polyethylene lined pot used in the growth chamber. Yellow sweet

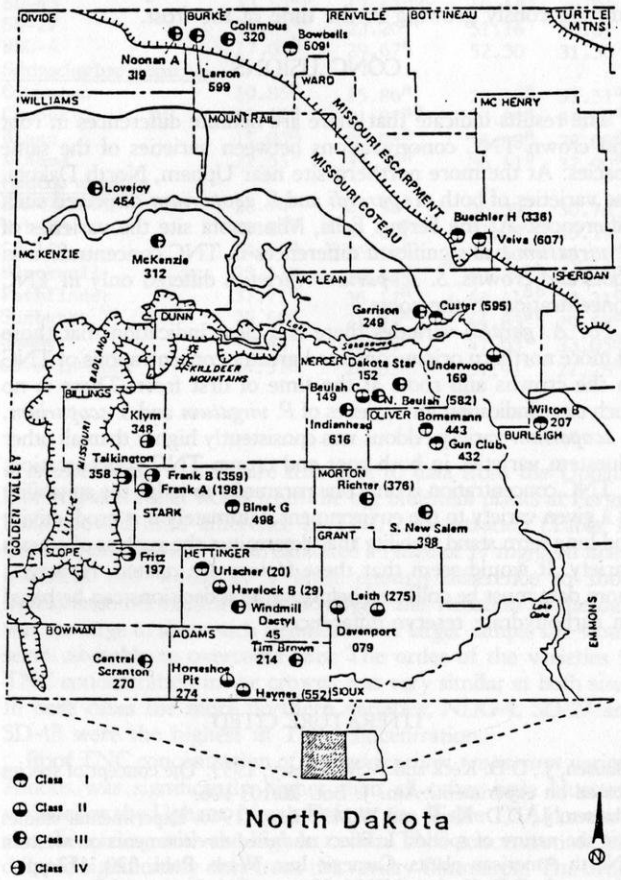

FIG. 1. The site classification of the 35 abandoned surface mined sites sampled by Project Reclamation in 1982 and 1983.

clover [*Melilotus officinalis* (L.) Lam] and western wheatgrass (*Agropyron smithii* Rybd.) were grown separately with three different fertilizer treatments. Treatments consisted of an untreated minespoil i.e., no fertilizer applied (control), a single application of NPK at the rates of 75, 50, and 25 μg/g spoil, respectively (F_1 treatment), and at 150, 100, and 50 μg/g spoil, respectively (F_2 treatment). Each treatment was reproduced in triplicate. The plants were grown in environmentally controlled growth chambers under 25° C day/15° C night temperatures, 12 hour photoperiod and 50% relative humidity. After seedlings emerged, the pots were thinned to 6 seedlings in each pot and water was added as needed to maintain approximately 60% water holding capacity. After 6 weeks of growth, the aboveground plant tissue was harvested at ground level, washed with deionized water, dried in an oven at 60 C for 48 hours and weighed.

An additional set of pots containing strongly acid spoil material of varying pHs were planted with yellow sweet clover [*Melilotus officinalis* (L.) Lam]. This additional experiment was to determine the relationship between pH and biomass produced in unfertilized and F_2 treatments.

TABLE 1. Classification of abandoned mine land sites and spoil material with reference to ease of difficulty for rehabilitation.

SITE DESCRIPTION	SITE CLASSIFICATION	SPOIL MATERIAL CLASSIFICATION	CHARACTERISTICS
Easily Rehabilitated Sites	Class I	a	Near neutral pH: 6.4 - 7.5 Negligible salinity: EC < 4 mmhos/cm * Non-sodic: SAR < 12
Rehabilitation Problematic	Class II	b	Acid to neutral pH: 4.3 - 7.7 # Slight to moderately saline: EC = 4 - 10 mmhos/cm Non-sodic: SAR < 12
Difficult to Rehabilitate	Class III	c	Usually alkaline pH: 7.0 - 8.7 Mostly moderately to strongly saline: EC = 4 - 15 mmhos/cm Sodic: SAR > 12
Very Difficult to Rehabilitate	Class IV	d	Strongly acid pH: < 4.0 Varying salinity: EC < 1 - 21 mmhos/cm Varying sodicity: SAR 0.1 - 28 Toxic levels of aluminum

* Most Class I sites have surface spoils having SAR values of $\leq$ 1.0.

\# Salinity in Class II sites is associated with high levels of magnesium salts.

The water saturation and extraction method was used to determine the pH and electrical conductivity (EC) of the spoil material (Sandoval and Power 1977). This method also provided an extract for cation analyses. A Radiometer PHM51 meter was used for determining the pH. A Radiometer CDM-2e meter was used for determining the EC.

The anaerobic incubation method of Waring and Bremner (1964), modified by Powers (1980), was used to estimate the spoil material's mineralizable nitrogen with an ammonia electrode (Siegel 1980).

Ca, Mg, Na, K, and Al were determined on the spoil material's saturation extract by atomic absorption spectrophotometry (Perkin-Elmer Model 503) as outlined in the Perkin-Elmer Manual (1973). This allowed the Sodium Adsorption Ratio (SAR) to be calculated using the equation presented by Sandoval et al. (1973).

Phosphorus was determined by a method detailed by Knudsen (1980) which is a modification of Olsen et al. (1954). Zn was determined by DTPA extraction (Lindsay and Norvall 1978) and atomic absorption spectrophotometry (Perkin-Elmer Manual 1973).

RESULTS AND DISCUSSION

The sites sampled cover a large geographical area of North Dakota, ranging from the South Dakota border to the Canadian border and from the Montana border to the center of the state (Fig. 1). Consequently, the sites vary in their climate, soil parent materials, topography, and time since disturbance which, in turn, help determine the current and potential type and quantity of vegetation found on abandoned mine spoils.

Vegetational cover and plant species richness were most limited on minespoils having excess acidity or salinity (Nicholson et al. 1984). Several abandoned uraniferous lignite mines in Billings, Stark, and Slope counties of North Dakota contained mine spoils that were extremely acid (pH < 4.0). Under such conditions, potentially toxic metals, such as aluminum (Al), become soluble. Approximately 1 ppm aluminum in the soil solution is toxic to the roots of aluminum sensitive plant species (Lignon and Pierre 1932). We have found that "saturated extracts" from these sites contained more than 500 ppm soluble aluminum, and one subsurface sample from the Frank A (198) site contained over 4,000 ppm soluble aluminum (Nicholson et al. 1984).

A second important factor limiting plant establishment on abandoned mine spoils in North Dakota is a deficiency in water availability, which is directly and indirectly influenced by the amounts of total soluble salts and sodium ions present in the spoils. High amounts of total soluble salts will decrease or reverse the osmotic gradient between root cells and the soil solution thereby making absorption by roots more difficult and impossible in excessively saline spoils (EC > 8 mmhos/cm) (Sandoval et al. 1973).

Thirdly, the amount of sodium on the cation exchange sites is particularly important because it negatively alters the physical properties of mine spoils. Sodicity or high amounts of exchangeable sodium (SAR > 12) will cause the clay in spoils to disperse and clog spoil pores. The result is a compact and crusted spoil surface that severely decreases the infiltration of rain and thereby slows soil water recharge.

These major factors: reaction, salinity, and sodicity, measured as pH, electrical conductivity (EC), and sodium adsorption ratio (SAR), were used as the basis for the development of a system to classify abandoned surface mined sites. The four major classes and the four subclasses are defined in Table 1.

Mine sites located in west central North Dakota containing acid spoils were placed in Class IV, defined as having spoils of pH < 4.0. Mine sites having both saline and sodic spoils are classified as Class III sites, i.e., if any samples had SAR values exceeding 12 and EC values exceeding 4 mmhos/cm. Mine spoil salinity was found to be highly variable within sites, therefore, mean electrical conductivity (EC) values were used to determine if a site was placed into Class I or Class II (Table 1). It was found that slope aspect was related to the salinity of spoils within Class III sites. Several sites had Class A or B mine spoils on their north-facing slopes and Class C spoils on their south-facing slopes. When classifying each mine site, we were conservative, and used the most acid, saline, or sodic spoil sample collected from the site to determine mine site classification (Table 1).

Plotting each classification class on surface geology and bedrock geology maps of North Dakota revealed that the non-saline and non-sodic Class I sites are located in the glaciated area of North Dakota resulting in overburden material dominated by glacial till. Exceptions to this are Binek G (498) and Urlacher (20) sites, but these two sites are adjacent to major rivers in western North Dakota with alluvium probably contributing to these favorable properties. Comparing the bedrock geology with the four major classification classes reveals that Class I and Class II sites are most commonly

TABLE 2. Chemical analysis and source of mine spoil mixtures used in growth chamber experiments. Refer to text for explanation of mine spoil classes.

Mine Spoil Class		pH	EC mmhos/cm	SAR	N (ppm)	P (ppm)	K (me/L)	Zn (ppm)	Spoil Character and Source
I a	range	6.68-7.70	0.9- 4.1	0.1- 8.3	1.6-38.0	1.1- 8.0	8.4-31.1	0.2- 2.6	TYPIC, neutral, non-sodic and
	mean	7.20	2.1	1.0	16.1	3.8	19.1	0.9	non-saline spoils from Class I
(n=18)	s	0.24	1.0	1.9	12.0	1.8	7.1	0.7	sites.
II a	range	6.73-7.52	0.8- 4.0	0.2- 0.4	5.4-24.7	2.5-35.6	13.5-41.8	0.2- 4.2	Neutral, non-sodic and non-
	mean	7.06	2.6	0.3	12.5	10.5	25.6	1.4	saline spoils from Class II
(n=8)	s	0.29	1.3	0.1	6.3	11.9	10.2	1.3	sites.
III a	range	6.99-7.44	0.9- 3.9	0.2- 4.8	4.6-56.0	1.1- 6.6	14.0-40.0	0.2- 1.9	Neutral, non-sodic and non-
	mean	7.22	2.7	1.8	19.0	3.8	20.8	0.8	saline spoils from Class III
(n=9)	s	0.15	1.3	1.7	16.4	1.9	7.7	0.5	sites.
IV a	range	6.84-7.20	0.6- 0.7	0.1- 0.2	10.4-13.1	3.8- 5.2	3.5- 4.0	0.2- 0.3	Neutral, non-sodic and non-
	mean	6.98	0.7	0.2	11.8	4.5	3.8	0.2	saline spoils from the Class
(n=2)	s	0.25	0.1	0.1	1.0	1.0	0.4	0.0	IV Fritz site.
II b	range	4.61-7.13	4.1- 8.6	0.3- 3.5	3.3-22.3	3.8-14.2	11.6-45.0	1.7-13.6	TYPIC, acid to neutral non-
	mean	5.28	5.5	1.3	8.6	7.2	23.6	5.4	sodic, saline spoils from Class
(n=6)	s	1.08	1.3	1.2	7.2	4.2	12.3	5.4	II sites.
III b	range	6.87-8.61	3.8-13.8	4.0-11.0	4.3-18.6	1.9-12.8	9.1-48.0	0.1- 2.9	Neutral to alkaline, non-sodic,
	mean	7.25	5.9	8.2	9.0	4.7	33.1	1.4	but saline spoils from Class
(n=11)	s	0.54	2.8	2.2	4.5	3.1	15.0	1.3	III sites.
III c	range	6.77-8.30	4.0-15.0	14.6-49.0	1.2-11.8	1.1- 9.4	27.8-94.8	0.8-10.9	TYPIC, alkaline, sodic and
	mean	7.34	10.3	30.0	5.8	3.2	57.1	2.6	saline spoils from Class III
(n=14)	s	0.48	3.2	9.6	3.0	2.3	24.0	3.6	sites.
IV c	range	4.15-4.19	1.9- 3.2	14.6-19.8	2.3- 2.5	54.3-57.0	10.2-14.9	0.3- 0.4	Strongly acid, non-saline, but
	mean	4.17	2.6	17.2	2.4	55.6	12.6	0.4	sodic spoils from Class IV
(n=2)	s	0.03	0.9	3.7	0.2	1.9	3.3	0.0	Frank B and Klym sites.
IV d	range	2.59-3.65	3.7-14.2	0.2- 3.6	4.3-26.1	5.2-55.6	4.0-29.3	1.3- 8.1	TYPIC, very strongly acid, non-
	mean	3.07	6.9	1.4	15.0	29.2	12.4	4.1	sodic but saline spoils from
(n=4)	s	0.50	4.9	1.6	10.3	20.6	11.5	3.5	Class IV sites.
Prairie	range	6.37-6.50	0.6- 1.2	0.1- 0.3	49.0-53.4	3.8-12.1	13.6-25.2	0.8- 1.2	Representative slightly acid,
	mean	6.43	0.9	0.2	51.2	8.0	19.4	1.0	non-sodic and non-saline native
(n=2)	s	0.1	0.4	0.1	3.1	5.8	8.2	0.3	prairie topsoil.

associated with areas having little Sentinel Butte material and dominated by the Bullion Creek and Slope Formations. Class IV sites are found in association with the Sentinel Butte Formation. Class III sites are found in association with both Sentinel Butte and Slope formations and to a lesser extent, the Bullion Creek Formation.

Mine spoil characteristics varied widely within mine site classifications (Table 2) as did the potential productivity (Table 3). Further, spoil material that is non-sodic, non-saline, and neutral (Class I characteristics) may be found at sites of all four classes. Therefore, in our effort to accurately represent the variability present at the abandoned mine land sites, four subclasses were created which are represented by a, b, c, and d. The numerals I, II, III, and IV refer to the site classification as defined in Table 1 and illustrated in Fig. 1. The subscripts a, b, c, and d refer to the spoil material characteristics and are defined in Table 1. The expanded classification resulted in nine groupings of abandoned mine land spoil material (Tables 2, 3, and 4). Each grouping is represented by a numeral, depicting the site's characteristics, and a lower case letter, depicting the variability of spoil material found on the sites that compose each of the four major classes. The selected chemical properties and characteristics as well as the potential productivity of the nine mine spoil groupings were compared to those for the sampled native prairie sites (Tables 2 and 3).

Mine spoils from all sites contained extremely low amounts of mineralizable-N and extractable P as compared to the native prairie sites (Table 2). The consistent and high response of both

FIG. 2. Relationship between *Melilotus officinalis* yield and mine spoil pH on strongly acid spoil material. Two treatments, no fertilizer (control) and F_2 (NPK, treatment) were used.

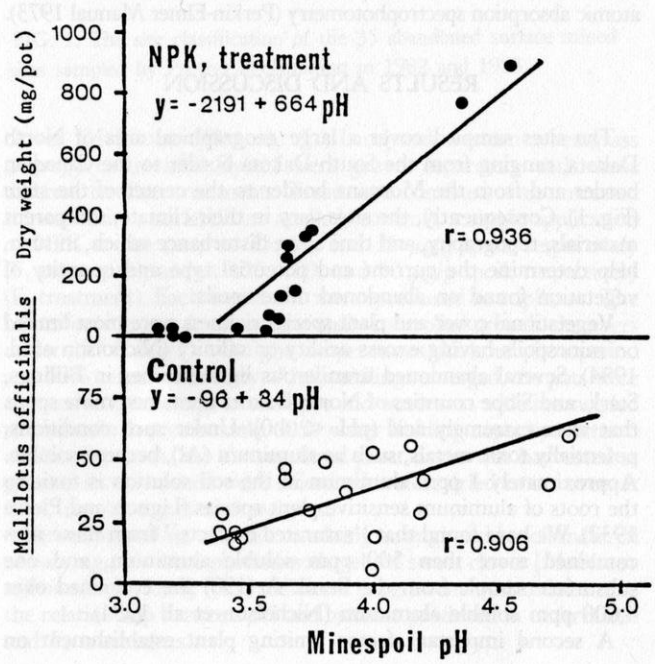

TABLE 3. Dryweight yields for two test crops grown in mine spoil and representative native prairie topsoil from western North Dakota, under controlled temperature, humidity and moisture. All yields are mg/pot. F_1 = Fertilizer rate -1, F_2 = Fertilizer rate -2. Refer to text for details.

Mine Spoil Class		*Agropyron smithii*			*Melilotus officinalis*		
		Control	F_1	F_2	Control	F_1	F_2
I a	range	28-169	107-637	213-950	57-262	357-1128	393-1622
	mean	61	370	637	150	789	975
(n=18)	s	34	168	224	62	235	312
II a	range	45- 76	168-506	217-938	92-211	356-1118	565-1338
	mean	58	351	575	139	658	895
(n=8)	s	11	152	272	43	302	272
III a	range	20- 89	180-474	383-923	60-249	183- 883	501-1394
	mean	52	342	642	110	586	952
(n=9)	s	24	93	152	61	271	316
IV a	range	51- 69	226-261	217-938	160-484	869- 910	829- 848
	mean	60	243	575	322	890	838
(n=2)	s	13	25	272	229	29	13
II b	range	24-127	111-534	116-641	70-286	148-1046	243- 896
	mean	70	393	454	147	596	750
(n=6)	s	34	154	191	80	287	256
III b	range	21- 94	76-664	153-814	37-314	100- 767	330-1016
	mean	51	333	463	111	467	667
(n=11)	s	25	226	221	77	223	258
III c	range	24-189	143-679	128-679	40-275	69-1149	110-1495
	mean	68	318	448	82	360	425
(n=14)	s	46	172	247	64	287	391
IV c	range	46- 55	329-338	356-410	57-140	774- 887	998-1065
	mean	51	334	383	98	830	1031
(n=2)	s	7	6	38	59	80	47
IV d	range	0- 26	0- 34	0-116	0- 46	0- 144	0- 295
	mean	15	25	56	26	72	147
(n=4)	s	11	16	52	22	83	154
Native	range	97-204	463-633	763-854	193-763	1093-1138	1139-1385
	mean	150	548	808	478	1120	1262
(n=2)	s	76	120	64	403	32	174

test crops to NPK fertilization (Table 3) reiterates the importance of nitrogen and phosphorus deficiencies in mine spoils of western North Dakota (Safaya and Wali 1979, Malakondaiah et al. 1981).

Yields generally decrease as the mine spoil becomes more saline and sodic (Table 3). Unusually low yields were observed on the very strongly acid spoils from Class IV sites.

A correlation analysis was performed to determine the relationship between the test crop yields and selected spoil chemical parameters, i.e., pH, electrical conductivity (EC), potassium (K), and zinc (Zn). Zinc was included because the DTPA extractable Zn in many spoils was found at levels considered deficient in agricultural soils (< 0.5 ppm) (Viets and Lindsay 1973). *Agropyron smithii* yields were significantly correlated with DTPA extractable Zn in neutral, non-sodic, and non-saline mine spoils (Table 4). Both test crops showed yields which correlated significantly and positively with DTPA extractable Zn after they had received a complete fertilizer treatment. Therefore, Zn deficiency may have been induced by the addition of phosphorus fertilizer (Murphy

TABLE 4. Correlation coefficients for test crop yields with selected chemical parameters under growth chamber conditions.

Mine Spoil Class	Treatment	*Agropyron smithii* pH	EC	K	Zn	*Melilotus officinalis* pH	EC	K	Zn
I a	Control	.152	-.201	-.024	.237	.109	.167	.353	.168
	F_1	.028	.439	.242	.548*	.246	.237	-.066	.061
(n=18)	F_2	-.341	.612**	.448	.517*	.205	.032	-.027	.304
II a	Control	.137	-.342	.007	.769*	.159	-.318	-.194	-.457
	F_1	-.554	.319	.359	.516	.165	.116	.806*	.494
(n=8)	F_2	-.517	.262	.313	.747	-.268	.082	.454	.780*
III a	Control	-.451	.095	.403	.447	-.534	-.072	.280	.655
	F_1	-.185	.017	.623	.438	-.080	.111	-.630	-.092
(n=9)	F_2	.170	.715*	-.146	-.096	-.276	.139	-.401	.063
II b	Control	-.764	-.027	.360	.761	-.115	-.468	-.177	-.088
	F_1	.220	-.912*	.183	-.274	-.199	-.716	.177	.157
(n=6)	F_2	.562	-.930**	.197	-.581	.378	-.980**	.155	-.406
III b	Control	-.509	-.255	-.764**	.448	-.471	-.292	.506	.451
	F_1	-.148	-.299	.436	.497	-.672*	-.451	.263	.843**
(n=11)	F_2	-.161	-.153	.549	.438	-.700*	-.410	.630*	.731*
III c	Control	-.228	-.061	.438	.674**	-.326	-.366	.406	.760**
	F_1	-.496	.073	.319	.596*	-.030	-.291	.645*	.705**
(n=14)	F_2	-.486	.294	.241	.490	-.318	-.134	.702**	.834**
IV d	Control	.929	-.828	.816	.955*	.894	-.787	.560	.206
	F_1	.994**	-.983**	.520	.427	.719	-.559	.583	.308
(n=4)	F_2	.803	-.665	.806	.666	.767	-.629	.528	.204

F_1 = NPK at 75, 50, 25 µg/g spoil, respectively. * = $p < .05$

F_2 = NPK at 150, 100, 50 µg/g spoil, respectively. ** = $p < .01$

et al. 1981). Phosphorus induced Zn deficiency has also been reported for corn grown in alkaline (pH = 7.5) mine spoil from Illinois (Dancer 1985). Crop yield correlations with DTPA extractable Zn were strongest in the most alkaline and saline mine spoils from Class III sites.

As expected, crop productivity was negatively correlated with salinity, as measured by EC, in saline minespoils from Class II and Class III sites. It is notable that the high rate of fertilizer (F_2) sometimes increased the correlation between yield and salinity, presumably by increasing the soluble salt content of the minespoil.

The significant and positive correlation of yellow sweet clover with soluble potassium indicates that potassium may become deficient for plant growth after nitrogen and phosphorus deficiencies have been remedied with fertilizer, particularly in soils from Class III sites. The low levels of soluble K (Table 2) and its high correlation with plant growth in the strongly acid Class IV spoils (Table 4) was associated with the presence of jarosite, as documented elsewhere (Wagner et al. 1979).

An additional experiment using *Melilotus officinalis* to ascertain more precisely the relationship between plant yield and the pH of strongly acid mine spoil (Class IV) is illustrated in Fig. 2. Two previously used treatments, the control and F_2, were used for the additional experiment. Yellow sweet clover yields were significantly correlated with mine spoil pH and little, if any, growth or seedling establishment occurred when the pH was below 3.5. These results are consistent with observations made on strongly acid eastern U.S. mine spoils, where little or no plant establishment or growth of acid tolerant plants occurs at pH below 3.5 (Foy et al. 1980).

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WARM SEASON GRASSES - NEW AGRICULTURAL CROP FOR THE CORNBELT

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Abstract. A principal use for corn in the United States is as a feed for beef and dairy cattle. As ruminants, cattle are also capable of digesting lignocellulose, although at a much lower rate and efficiency than grain. Thus, beef production from corn is faster, more efficient, and more economic than is beef production from lignocellulose. However, corn production is associated with high rates of topsoil erosion and is heavily dependent upon the use of chemical pesticides. New postharvest treatment processes are now being developed that increase the digestibility of native lignocellulose by ruminants to a level similar to that obtained with corn. This technology offers the possibility of using lignocellulose in place of grain as a dietary energy source for cattle. After such treatment, the amount of digestible cattle feed that can be produced per hectare of prairie grass is at least equivalent to the amount of feed that can be produced per hectare of corn. Thus, the way is open for future development of tall grass prairie as an erosion-resistant, ecologically stable agricultural crop for use on erosion-prone cropland in the Midwestern Cornbelt.

INTRODUCTION

The deep, fertile topsoils of the American Midwestern plains have played a major role in making the United States the leading agricultural producer in the world. These rich prairie soils were formed over thousands of years from the annual growth and decay of native, warm season grasses that once covered perhaps 200 million hectares (500 million acres) between the Appalachian and Rocky Mountains.

Most of the original stands of native prairie have now fallen victim to modern, tillage-based farming practices. The depth of the prairie topsoil and its high productivity once led farmers to believe that its fertility was practically inexhaustible. The fallacy of this assumption became disastrously apparent in the 1930's, and we now know that to prolong the productive life of our topsoil legacy, careful adherence to appropriate erosion control practices is essential. Nevertheless, the realities of the modern agricultural economy have resulted in widespread cultivation of even marginal cropland, where the rate of topsoil erosion far exceeds the rate of new topsoil formation. It is clear that the present situation cannot persist for long without serious consequences for the future agricultural productivity of the United States (Pierce et al. 1983).

The crops produced on marginal, erosion-prone cropland are not an insignificant part of total U.S. crop production (e.g., Table 1). Increasing demand for food by an expanding world population, as well as economic pressures on farm operators, dictate that any alteration of production practices to reduce soil erosion must not seriously diminish total crop output. Conservation tillage practices satisfy this requirement, and can be an effective method for reducing erosion to tolerable levels (Moldenhauer et al. 1983). However, current conservation tillage methods require the use of high levels of herbicides and insecticides to obtain acceptable crop yields (Hinkle 1983). This dependence upon chemical methods of weed and pest control carries with it the potential for long-range environmental problems, including pollution of rivers, streams, lakes and groundwater supplies. Thus, conservation tillage must be considered to be a short-term solution to the soil erosion problem.

A more suitable, long-term solution could come from the identification of new or alternative crop species possessing characteristics that make them inherently more resistant to soil erosion. Substitution of such new crops for conventional row crops on marginal land would reduce erosion without removing that land from the production base.

If we are to identify suitable alternative crops for these marginal

TABLE 1. Annual corn production and soil erosion in six midwestern states.

State	Corn production[a]	Cultivated cropland[b]		Topsoil loss[b]
		Req. conservation	Total	
	(1000 MT)	(1000 Hectares)		(1000 MT)
Illinois	38,816	5,029	9.650	143,775
Indiana	20,753	2,145	5,393	59,659
Iowa	40,502	7,068	10,701	235,369
Missouri	5,215	3,571	5,900	140,367
Nebraska	19,609	4,184	8,380	106,120
Ohio	12,091	1,400	4,762	36,498
TOTAL	136,986	23,397	44,786	721,788
U.S. TOTAL	213,750	85,216	167,172	1,682,828
% of U.S. TOTAL	64.1%	27.5%	26.8%	42.9%

[a] USDA, 1983. [b] USDA, 1977.

croplands, it is necessary to first determine what crops are presently produced there, and how those crops are being utilized. Soil erosion in the U.S. is disproportionately concentrated in the Midwestern cornbelt, where 27% of the nation's cultivated cropland accounts for 43% of the nation's annual topsoil loss (Table 1). More than half of the cultivated cropland in the Cornbelt now requires some type of conservation treatment to reduce erosion rates to acceptable levels. In the Midwest, excessive soil erosion on marginal cropland is almost always associated with the production of row crops - principally corn (USDA 1977). Almost 90% of the 214 million metric ton corn crop produced each year in the U.S. is fed to livestock, either domestically or after export to foreign markets (USDA 1983). About a third of the domestically utilized corn grain is fed to beef and dairy cattle alone, with the balance going primarily to feed hogs and chickens. A small amount (5%) also goes for industrial use and direct human consumption (USDA 1983).

WHY FEED CORN TO CATTLE?

As ruminants, cattle are among the handful of animals with the ability to utilize cellulose as their principal food source. Nevertheless, grain is used as a major component in cattle diets today because grain-fed cattle gain weight much faster and can be marketed sooner than cattle fed a cellulose-based diet (CAST 1980). The reasons for this difference are complex, but can be traced in large part to the fact that cellulose in nature is generally found in close association with lignin, an intractable polymeric material that cements individual cellulose fibers together and strengthens plant cell walls. The resulting lignocellulose complex is unusually resistant to degradation by enzymes and microorganisms, severely limiting its breakdown in the rumen (Van Soest 1982).

A great deal of research effort has been directed towards finding ways to improve the digestion of lignocellulose by ruminants (Sundstol and Owen 1980). A large number of mechanical, chemical and biological pretreatments have been developed that improve lignocellulose digestibility significantly, although levels of digestibility comparable to those exhibited by grain have been difficult to obtain. Recently we have reported the development of a chemical pretreatment in which half or more of the lignin can be removed from a variety of lignocellulosic substrates, yielding a product in which the cellulose is almost completely digestible in the rumen. This process, which is modelled after the natural delignification mechanism of wood-rotting fungi, involves treating lignocellulosic material with a dilute hydrogen peroxide solution for a period of several hours (Gould 1984). In feeding trials conducted at the University of Illinois, sheep fed hydrogen peroxide-treated wheat straw gained weight at the same rate as sheep fed a corn-based diet. Sheep fed a diet of untreated wheat straw lost weight during the trial (Kerley et al. 1985). These and similar studies indicate that it is possible for ruminant animals to gain weight on a lignocellulose-based diet as rapidly and efficiently as animals fed a grain-based diet, provided the lignocellulose is suitably treated beforehand to increase its digestibility.

SOURCES OF LIGNOCELLULOSE

Assuming treatment processes such as the one described above can be made economically feasible, a number of possible sources of lignocellulose are available for use in cattle feed as a substitute for corn. These include:

1. **Crop Residues**. Large quantities of corn stalks, wheat straw and other plant residues are generated each year as byproducts of grain production (Miller and Eisenhauer 1982). In some regions of the U.S. conditions are such that collection and utilization of a substantial portion of these residues are feasible. In most areas, including the Cornbelt, however, it is necessary to leave at least half of the residues on the fields to maintain soil tilth and help control erosion (Lindstrom et al. 1981).
2. **Wood Chips, Sawdust, etc**. Wastes from the lumber and paper manufacturing industries are readily available in some parts of the country, although these areas are generally not close to major cattle producing areas.
3. **Waste Paper**. Each year immense quantities of waste paper are generated in the U.S. The usefulness of this abundant resource as a feed is limited, however, by the necessity to remove or detoxify inks, colorings, and other additives associated with most waste paper.
4. **Biomass Crops**. These are crops that could be produced specifically for their lignocellulosic component. Factors important in selecting such a crop include: high yield, economical production and harvesting characteristics, compatibility with soil and climatic restraints, resistance to soil erosion, and resistance to diseases, pests and drought.

PRAIRIE GRASSES FOR THE CORNBELT

Of the alternatives listed above, only biomass crops offer sufficient potential as a source of lignocellulose to replace a significant portion

TABLE 2. Five year average annual biomass production by native warm season grasses.

Grass	Common Name	Yield[a] (dry metric tons/ hectare)
Sorghastrum nutans	Indian grass	13.5-18.0
Andropogon gerardi	Big bluestem	15.7-18.0
Panicum virgatum	Switchgrass	11.2-18.0

[a] Roundtree, 1977 and USDA, 1981

of the annual grain production in the Cornbelt. A number of biomass crops are now being developed for other purposes (e.g., sweet sorghum, kenaf, fast growing poplar trees, etc.). It is important to remember that native vegetation tends to use water efficiently, and it is rare to find a field crop that, even with heavy fertilization, will exceed the biomass productivity of the natural ecosystem it replaced. The average total biomass (grain plus lignocellulose) produced each year by corn in the Midwest is approximately 13.5 metric tons/hectare (6 tons/acre) (USDA 1983, Lindstrom et al. 1981). The average harvestable biomass produced by prairie grass species once indigenous to the same region ranges from 11.2 to 18 metric tons/hectare (5-8 tons/acre) (Table 2).

Based upon the foregoing, we propose that prairie grasses such as big bluestem, switchgrass and Indian grass be considered as new biomass crops for the Cornbelt, to be planted on marginal, erosion-prone cropland that is now used for the production of corn. The lignocellulose produced each year by the grasses could be harvested, suitably treated to increase its digestibility, and then used in lieu of corn as a high energy feed for ruminants.

Warm season grasses offer a number of advantages over corn for marginal croplands:

1. Corn is an annual plant - fields must be prepared and reseeded each year, at considerable expense of both time and money. Warm season grasses, on the other hand, are perennials - once they have become established, no further tillage or reseeding is required.
2. Corn production leaves the soil bare for more than 6 months of the year, exacerbating erosion tendencies already inherent in the topography of the field. In contrast, the deep, extensive root system of native prairie grass is extremely effective at retaining soil particles (Weaver 1968), and, in conjunction with the permanent ground cover these plants provide, effectively eliminates soil erosion.
3. A field of corn is an unstable ecosystem, with large areas of bare soil between the rows of plants. Modern corn varieties are such poor competitors in a natural ecosystem that the survival of corn as a species is now considered to be completely dependent upon man (Leonard and Martin 1963). It is necessary to severely restrict interspecies competition within a corn field by employing fuel-intensive cultivations and/or by applying chemical herbicides. Indeed, more than half of the herbicide used each year in the U.S. is applied to corn fields (Table 3). Warm season grasses, in contrast, form a stable climax ecosystem that covers the entire field and does not need artificial protection from interspecies competition. This factor alone would substantially reduce production costs by eliminating the need for cultivation and herbicides. Furthermore, prairie grass communities are remarkably resistant to pest infestations (Weaver 1954), eliminating the need for toxic chemical insecticides and their associated environmental problems.
4. Prairie grasses are much more resistant to drought than cereal crops such as corn (Weaver 1954), reducing the annual risk of crop loss.
5. The production of warm season grasses would require a great deal less management than the production of corn. A typical corn production system can require the farmer to make as many as seven passes over the field, including plowing, disking, harrowing, planting, cultivating, application of herbicide, insecticide and fertilizer, and harvesting. In contrast, the lignocellulose produced by a prairie grass crop would be harvested once a year, in the fall, after the dormant plants have field-dried. Harvested prairie grass could be stored in the field in weather-resistant round bales or stacks. The only other time the farmer would need to be on the field would be for the application of fertilizer.

TABLE 3. Pesticide utilization in U.S. Agriculture.

Crop	Annual usage[a]	
	Herbicides	Insecticides
	(% of U.S. total)	
Corn	53	20
Soybeans	21	5
Wheat	6	5
Cotton	5	40

[a] Eichers, 1981. Total U.S. usage (herbicides plus insecticides) in 1981 was 384,545 metric tons.

TABLE 4. Estimated annual production costs for corn and prairie grass in Illinois.

Item	Corn[a] (7.8 MT/hectare)	Prairie Grass (13.5 MT/hectare)
	(dollars/hectare)	
Seed	44	0[b]
Pesticide	40	0
Fertilizer (N,P,K,lime)	128	150
Machinery:		
Maintainence & fuel	79	50
Depreciation & interest	124	100
Operating capital	20	10
Drying (fuel, etc.)	37	0
Labor	52	59
Management	35	24
Storage	67	0
Miscellaneous	37	37
TOTAL cost per hectare	$663	$430

[a] Hinton, 1981.
[b] One-time seeding costs for initial establishment of the grass are not included.

All of these factors contribute towards providing a substantial economic incentive for substituting prairie grasses for corn on marginal, erosion-prone cropland. Estimates of annual production costs for each crop are shown in Table 4. These estimates indicate that in Illinois it would be possible to produce 13.5 metric tons/hectare (6 tons/acre) of prairie grass for about two-thirds the cost of producing corn at 7.8 metric tons/hectare (125 bushels/acre). After suitable treatment to increase digestibility, the amount of high-energy cattle feed in 5.5 metric tons (6 tons) of warm season grass would be equivalent to that in 3.2 metric tons (125 bushels) of corn grain. With higher levels of biomass production, correspondingly higher equivalent corn yields could be obtained (Fig. 1).

There are also economic incentives at the national level for replacing corn as a crop on erosion-prone cropland. The Federal Government now spends enormous sums each year to encourage soil conservation by paying farmers to idle marginal acreage. To the extent that permanent, erosion-resistant crops such as prairie grass were established on this marginal cropland, further incentive payments would become unnecessary.

Reintroduction of prairie grasses to the soils of the American Midwest presents an opportunity to reverse the serious problems of soil erosion and pesticide pollution that now plague row crop-based agriculture in this region. As world population increases and demand for food escalates, the pressure to increase food production from a finite or dwindling land resource base will only exacerbate these problems. The productivity of American agriculture rose sharply between the 1930's and the late 1960's, but now the rate of productivity increase has slowed dramatically. The large increase in productivity of cereal crops during the past 50 years can be attributed to three major factors: more intensive use of fertilizer, development of chemical pesticides, and selection for crop plants that preferentially partition photosynthetic products into grain. This shift towards starch production comes at the

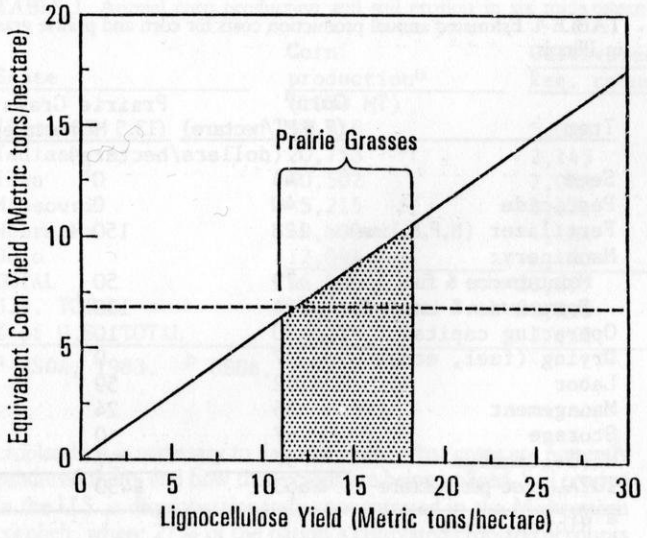

FIG. 1. Lignocellulose production and its equivalent corn yield assuming that 70% of the original dry weight of the lignocellulose is carbohydrate that has been rendered digestible by a suitable pretreatment (Gould 1985). The horizontal dashed line indicates the average U.S. corn yield in 1982 (USDA 1983).

expense of root, stem, and leaf production, and results in plants less able to compete for light and water (Good and Bell 1980). If we are to sustain our present high level of agricultural productivity into the next century, we must move away from crops dependent upon ever more expensive methods of limiting interspecies competition, and begin to utilize crop species that are inherently efficient competitors. Substitution of prairie grasses for corn on marginal cropland in the Midwest would be an important first step in this direction.

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Part 9. LANDSCAPING WITH PRAIRIE PLANTS

MADISON, WISCONSIN'S "NATURAL LAWN ORDINANCE": AN HISTORIC OVERVIEW

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Abstract. This paper presents a brief history of the revision of the Madison, Wisconsin lawn mowing and noxious weed ordinance. The purpose of these efforts was to legalize prairie grass plantings as well as other non-traditional forms of landscaping. Suggestions are set forth on how interested parties might seek to revise similar ordinances in light of the Madison experience. Also discussed are the objections to naturalized landscapes that persist to this day. Based on a review of related scientific literature and design perspectives, counter arguments to these objections are presented.

INTRODUCTION

The active use of indigenous grassland communities as a landscaping medium is a relatively recent phenomenon. This unfamiliar form of urban/suburban landscaping has also brought controversy and conflict between proponents of individual rights and those who feel that their well being is threatened. In the light of scientific evidence and the experience of many landscape architects these perceived threats are inaccurate.

In this paper I will discuss the process by which the city of Madison's "Natural Lawns" ordinance was passed, offer some responses to continuing objections and suggest considerations that might be incorporated into the development of a more enlightened civic attitude toward prairie plantings.

Wisconsin citizens have a history of pursuing clarification and liberalization of noxious weed statutes. These statutes attempt to regulate the height that turf grass is allowed to grow before mowing is required and list plants that are considered noxious. These plants include agronomic weeds for the most part but can, at local discretion, include such genera as the goldenrods (*Solidago* spp.) and the milkweeds (*Asclepias* spp.).

In the early 1970's the Wisconsin Natural Beauty Council and others worked for changes especially to promote the growing of indigenous prairie grasses. During this period a high school prairie planting was mowed, and individuals were cited, threatened with jail, and even brought to trial for growing prairie plants and/or prairie plants mixed with old field exotics.

THE MADISON, WISCONSIN ORDINANCE

In 1976 an ordinance to allow prairie grass planting was introduced into the Madison, Wisconsin Common Council and was defeated. In 1977, another proposal was put forth and subsequently referred to an ad-hoc committee. The committee was made up of landscape professionals, lay people, biologists, city staff (building inspection and parks departments) and alderpersons. The charge of the committee was to determine how to encourage natural landscaping and how to regulate it. The charge reflected that basic conflict between those who wanted no regulations at all and those who would accept no unmowed grass over 8″ in height.

Disputes included the nature of herbaceous plantings at property lines, costs (both to the individual and the city), the extent and nature of any plan or drawing to be submitted, permit and revocation procedures, neighbor approval/disapproval methods and procedures, and an inclusion of a clause rescinding the ordinance after two years. Opposition from some members of the city fire department was extremely strong on many items.

Meetings were then held with various city commissions, departments, and interested supportive individuals. These meetings proved to be very productive.

The ordinance was passed by the Common Council on October 17, 1978 by a vote of 13 to 7. An outcome of the passage was the publication of the booklet "An Introduction to Naturalized Landscapes" (Diekelmann and Bruner, nd.). The booklet explains how to use the ordinance, dispels many anti-naturalized landscaping myths, and demonstrates some ways natural landscapes might be integrated into more formal and traditional surroundings.

Briefly, the ordinance requires that individuals who are interested in a natural lawn submit a sketch to owners of property within 200 feet of the project. If more than 51 percent object, the application is rejected. However, the applicant may appeal to the city's Urban Design Commission. This commission is made up of landscape architects, architects, city staff and alderpersons. The commission may overturn the rejection, if the individual's landscaping pursuits are deemed legitimate.

At the time, confusion existed (and persists to this day) about which plants the proposed ordinance would cover. Many objected that the ordinance would require them to obtain a permit to grow any plant; when in fact the proposed ordinance clearly stated that only grass taller than 8″ in height was to be covered by its provisions. The text of the ordinance is included in the Appendix.

As of January 1985, there have been 28 applications, 2 of which have been disapproved. The ordinance has been re-enacted with the deletion of its expiration date. The feared wave of property neglect has not materialized.

The ordinance has served many purposes. It has lent legitimacy to prairie plantings; thus enabling a wider segment of the population to become familiar with the prairie. It has also helped schools that wanted to establish natural plantings. An additional outcome has been that it has protected people who do not plant prairies, but have chosen to landscape with lawn substitutes consisting of various combinations of native, exotic, and horticultural plants.

The ordinance is not without its negative aspects. Individuals who are improving environmental quality must devote time to a somewhat cumbersome procedure. In the opinion of many, prairies are the most desirable form of "lawn."

Although each situation will be different, I would like to offer some recommendations.

1. Involve all parties early in the effort to rescind or revise the legislation in question. It is quite possible that effective work during this first step will obviate the need for any ordinance at all. Include:
   - Supportive experts such as allergists, attorneys, botanists, entomologists, fire behavior specialists, landscape architects, media people, public relations people, and zoologists who can help develop credibility;

- Lay people who can lobby elected representatives;
- Government officials from elected bodies, building inspection, the fire department, forestry, the parks department, planning, and zoning boards, who can be helpful in determining the optimum procedures within the regulatory context.

2. Keep any demonstration projects to a manageable level such that:
   - They are kept scrupulously weed and litter free;
   - They truly consist of indigenous plants;
   - They have a representative cross-section of plants in bloom from early spring until late fall.

Despite the passage of the ordinance, objections to prairie plantings have persisted. Among the objections are:

1. Inordinately large populations of harmful animal life will be attracted.
2. There will be increased allergy suffering.
3. The proposed plants are weeds, will invade lawns and gardens, are a fire danger, and will cause property values to decrease.
4. Prairie plants are inappropriate with urban/suburban surroundings and appear unkept and unsightly.

These arguments can be viewed in the light of their contexts and a variety of counter arguments.

Inordinately Large Populations of Harmful Animal Life Will Be Attracted

Animal life, perceived as harmful, include species such as moles, rabbits, snakes and mosquitoes.

According to Gojmerac (1973), mosquitoes lay eggs "... in water or in areas that tend to flood." He adds that eggs "... of some species hatch in two or three days; others remain dormant for months or years, then hatch within minutes after being flooded." Mosquito larvae "... feed on bits of organic matter in the water changing to pupae in about one week. The adult mosquito emerges from the pupa in two or three days."

A review of Wisconsin's species of mosquitoes and their breeding areas may be found in Porter and Gojmerac (1970).

The presence of mosquitoes is a function of the availability of breeding places. Since mosquitoes can fly 10-15 miles from where they are hatched, prairie plantings are not specifically responsible for their presence. They can take refuge in any vegetation that provides protection from strong winds (P.J. Pellitteri, personal communication).

Other forms of wildlife can cause damage, but the damage is "... primarily associated with feeding activity, and to a lesser extent, related to denning, nesting, or roosting behavior ..." (Hawthorne 1983). Since 1973 the National Wildlife Federation has certified over 3,200 habitats in its backyard wildlife program. No damage to adjoining property has ever been attributable to wildlife attracted by the vegetation planted as part of this program (National Wildlife Federation Staff, personal communication).

In addition, the current University of Wisconsin Extension Service Professor of Wildlife Ecology has never received any complaints of damage from wildlife as a result of a nearby planting (S.R. Craven, personal communication).

There Will Be Increased Allergy Suffering

Herbaceous plants that are mainly responsible for pollen allergens occur in two general types of environments. The first is where there is repeated disturbance such as erosion or cultivation. The second is where there is a relatively permanent cover of non-indigenous grasses.

Although, according to Soloman and Mathews (1983), "... pollen allergens are not derived primarily from cultivated plants, human activities greatly affect the prevalence and health effects of these agents." They add "... humans have introduced many weedy grasses and broadleaf herbs, or 'forbs' - especially plantains, chenopods and amaranths - to North America from Eurasia."

The authors add that repeated disturbance of "... soil and plant cover are essential to the success of the ragweeds and weedy forbs that compete poorly with perennial species of open areas." Continuing, they note that "... in the Midwest, grain fields hold the highest density of short ragweed [*Ambrosia artemisiifolia*] growth." Thus we see that "... cultivated sites pose the greatest seasonal exposure risk for the ragweed pollen-sensitive subject."

Abandoned fields, pastures and unmowed lawns are the second type of environment that contain allergy producing agents. Soloman and Mathews (1983) state that in "... North America, most of the numerous wild native grasses shed little pollen, leaving relatively few introduced species as the source of grass pollinosis. Throughout Canada and the northeastern two-thirds of the United States, the bulk of wind-borne grass pollen is derived from the bluegrasses (*Poa pratensis* and *P. compressa*), orchard grass (*Dactylis glomerata*), timothy grass (*Phleum pratense*) and redtop grass (*Agrostis alba*)." They add that in the east "... perennial rye grass (*Lolium perenne*) and sweet vernal grass (*Anthoxanthum odoratum*) increase ..." in their contribution to the problem.

An additional finding is that in most areas the insect pollinated composites "... probably are negligible factors in pollinosis, although many patients still falsely ascribe their late summer symptoms to goldenrods" (Soloman and Mathews 1983).

The Proposed Plants Are Weeds, Will Invade Lawns and Gardens, Are a Fire Danger, and Will Cause Property Values to Decrease

> "Very rarely does a normal member of a native [plant] community become a weed within the geographical range of that community. In fact, a large majority of the worst weeds are exotic adventives, originating from a different continent" (Curtis 1959).

None of the major lawn and garden weeds in Wisconsin are plants that have been found to be prevalent prairie species according to Curtis (1959). Most are exotics imported from Europe and Asia.

Fire behavior is a complex subject affected by fuel loading, fuel moisture, wind, and fuel continuity. In addition, fires can produce sparks or embers that set others outside of the perimeter of the main fire (Chandler et al. 1983).

However, fire danger to buildings with wood siding by fires fueled exclusively by prairie forbs and grasses can be minimized if an adequate buffer strip is provided. In my experience a strip 2 meters wide has been adequate to protect buildings with painted wood siding from any damage by small controlled burns. These were fueled mainly by Indian grass (*Sorghastrum nutans*) and little bluestem grass (*Schizachyrium scoparium*). It should be noted that this distance may not be adequate to prevent injury to buds and needles of nearby woody vegetation.

The buffer strip can be of nonflammable materials such as stone or other paving materials. Alternately, herbaceous plants such as prairie smoke (*Geum triflorum*), alum root (*Heuchera richardsonii*), violets (*Viola* spp.), and Pennsylvania sedge (*Carex pensylvanica*) among others, may be utilized in this buffer. An additional possibility is a mowed and raked buffer of turf grass. These fuel breaks must be maintained free of plants that contribute to high fuel volume and/or high flammability (Chandler et al. 1983).

Popular materials such as recycled railroad ties and/or log rounds cut from unused utility poles are not recommended. According to Chandler et al. (1983) "... embers that cannot ignite leaves or sound wood will readily ignite ..." partly decayed old wood which can "... smolder for weeks until extinguished by rain or fanned into renewed activtiy by dry winds."

The subject of fire is too extensive to be covered in this paper. The reader is urged to consult works by Anderson (1979, 1982), Chandler et al. (1983), Rothermel (1983), Rothermel and Rinehart (1983), and Sneeuwjagt and Frandsen (1977) for expanded

discussions on the behavior and heat yields of grass fires.

The factors that contribute to the increase or decrease of property values are numerous and varied. In a recent case in southern Wisconsin, the claims of property owners near a naturalized planting that their properties were devalued were disallowed by the court. These claims were, in the judge's words, "hearsay" (New Berlin, City of v. Donald Hagar, 1976). Sites landscaped for wildlife and certified by the Natural Wildlife Federation have used the appearance of naturalized plantings as a positive sales factor. In my experience sites with prairie plantings have suffered no decrease in value or salability.

As prairie plantings gain legitimacy I am certain that they will contribute to the value of properties because of their energy conservation attributes as well as their natural beauty.

Prairie Plants Are Inappropriate With Urban/Suburban Surroundings and Appear Unkept and Unsightly

These objections may originate from viewing unmowed lawns. However, prairie plantings, especially those begun by seeding, look relatively unattractive and resemble a poorly established lawn for as much as three growing seasons. The importance of early attention to weeding and managing the planting as well as preparing the neighbors for the appearance during the first three years, cannot be over-emphasized. As a successful planting matures this appearance changes, and the planting begins to reflect some of the visual character of a native grassland.

The visual attributes of the prairie such as repetition through space and time, rhythm, harmony, modulation, suspense and resolution, emphasis and intervals, action and retardation and unity are those praised as integral components of the best fine art (Dewey 1934, Itten 1961, 1963).

Mature, well balanced and integrated prairie plantings do not appear unkept. Well designed plantings have a clear overall form and a complex diversity within that overall form (Diekelmann et al. 1986).

John Dewey (1934) observed that "... the habits of the eye as a medium of perception are being slowly altered in being accustomed to the shapes that are typical of industrial products ...." While this may be a desirable attribute of the built environment, it is not a necessity and may not be desirable for the planted environment.

Naturalized plantings are valuable in that they can inform us of different rhythms and dynamics. Rose (1980) has stated that "... to the extent that reality always remains complex and somewhat fluid, there is a continuing need to keep recalibrating the coordination of orientation as to time, place and person." Prairie landscaping can be a part of this process.

In Madison, Wisconsin the prairie future has been encouraged by the development of a municipal ordinance. Let us hope that the future holds experience similar to that which landscape architect Jens Jensen captured in his essay, "Dawn" (Jensen 1929). He described the appearance of grasses in autumn as:

> "... the most poetic of all - the foreground carpeted with delicate rose colored grasses, now made more vivid by the brilliant light of dawn, and amongst the grasses glistened millions of rosy diamonds, the first frost of the year."

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APPENDIX

Minimum Housing and Property Maintenance Code Sec. 27.05(2)(f)

(f) Landscaping, plantings and other decorative surface treatments, including common species of grass, shall be installed if necessary and maintained to present an attractive appearance in all court and yard areas. Except with prior application to and approval of a land management plan from the Building Inspection Division of the City of Madison, lawns shall be maintained to a height not to exceed eight (8) inches in length. Plantings shall be maintained so as not to present hazards to adjoining properties or to persons or vehicles traveling on public ways and shall be maintained so as to enhance the appearance and value of the property on which located and thereby the appearance and value of the neighborhood and City.

1. *Application for Natural Lawn*. Any owner or operator of land in the City of Madison may apply for approval of a land management plan for a natural lawn, one where the grasses exceed eight (8) inches in height, with the Building Inspection Division.
2. *"Land Management Plan"* means a written plan relating to management of the lawn which contains a legal description of the lawn upon which the grass will exceed eight (8) inches in length, a statement of intent and purpose for the lawn, a general description

of the vegetational types, plants, and plant succession involved, and the specific management and maintenance techniques to be employed. The management plan must include provisions for cutting at a length not greater than eight (8) inches the terrace area, that portion between the sidewalk and the street or a strip not less than four (4) feet adjacent to the street where there is no sidewalk, at least a three (3) foot strip adjacent to neighboring property lines unless waived by the abutting property owner on the side so affected.

All lawn and grass areas shall be cut between June 30 and October 15 when the Fire Chief, in his discretion, so orders consistent with his powers as granted in Chapter 34 of the Madison General Ordinances.

3. *Revocation of the Land Management Plan.* The Land Management Plan may be revoked for failure to comply with the requirements of Sec. 27.05(2)(f)2. Notice of intent to revoke a Land Management Plan shall be appealable to the Urban Design Commission. All applications for appeal shall be submitted within fifteen (15) days of Notice of Intent to revoke a Land Management Plan.
4. *Application Requirements.* Each application for a Land Management Plan shall be on a form provided by the Superintendent of Building Inspection Division. A copy of the application shall be mailed by the applicant or given personally by the applicant to each of the owners of record, as listed in the Office of the City Assessor, who are owners of the property situated in whole or in part within two hundred (200) feet of the boundaries of the properties affected. The Superintendent of the Building Inspection Division shall provide the list of the property owners who are to be notified of the application. The applicant shall certify, under oath, on a form to be furnished by the Superintendent of the Building Inspection Division, that such owners have been duly notified and the manner in which they have been notified. If, within fifteen (15) days of receipt of a copy of the application, at least fifty-one percent (51%) of such property owners file written objections to the application with the Superintendent of the Building Inspection Division, the Superintendent shall refer the application to the Urban Design Commission for hearing and decision.
5. *Application for Appeal.* The owner or operator of land in the City of Madison may appeal from a decision of the Superintendent of the Building Inspection Division refusing to grant a Land Management Plan. All appeals shall be to the Urban Design Commission of the City of Madison which shall hear such appeals once a month, March through September. All applications for appeal shall be submitted within fifteen (15) days of notice of denial of the Land Management Plan.

AN APPROACH TO RESIDENTIAL LANDSCAPING WITH PRAIRIE

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Abstract. This is a descriptive study of a process for developing residential and other small prairie plantings. Within a general approach factors are discussed of particular importance to prairie design: (1) the physical site conditions; (2) the temporal and physical structure of natural prairie communities; (3) the nature and arrangement of design elements in prairies; and (4) the desired size, scale and use of the planting. A prototypical planting is described in detail, with specific information about the assumptions made in the selection of forb and grass species and their numbers and proportions. The results of this approach are demonstrated by a planting in place since 1976.

INTRODUCTION

In order to create any landscape planting, it is necessary to decide:
1. Which species to use.
2. How many of each to include.
3. How to arrange them.

Several factors help to guide the selection, including:
1. Site conditions (particularly light, soil characteristics, and climate).
2. Practical considerations (the use of the area, species availability, time, money).
3. Educated personal taste.

For many designers, an added source of inspiration is the composition, structure, and dynamics of natural plant communities. One of the most interesting and diverse such communities is the North American prairie.

By studying and emulating natural models, an infinite variety of design expressions are possible. These may range from what are meant to be scientifically accurate restorations such as Greene and Curtis prairies at the University of Wisconsin Arboretum to simplifications meant to express the visual essence of the community (Dyas 1975, Morrison 1979). This paper will discuss an approach to residential landscaping which uses native prairie species in combinations that both emulate at least some of the functions and dynamics of natural prairies and satisfy aesthetic and practical concerns. Examples will be taken from the prairies of Wisconsin and northern Illinois, but the principles are widely relevant. The discussion will begin with the basic principles of this approach illustrated with a prototypical planting and continue with a description of an actual residential landscape incorporating these principles. As will be seen, this approach to prairie landscaping offers numerous opportunities for variation and personal expression.

GENERAL APPROACH

As outlined above, there are several factors which need to be considered in creating a landscape design. Important to prairie landscape design are: (1) the physical site conditions; (2) the temporal and physical structure of prairie communities; (3) the nature and arrangement of design elements in prairies; and (4) the desired size, scale and use of the planting.

Physical Site Condition

Prairies occupy a wide range of habitats. In southern Wisconsin and northern Illinois, for example, they are found both in river floodplains and on steep, thin-soil, south-facing bluffs. Specific species compositions change with environmental conditions. An understanding of general rainfall patterns and of the soil texture (sand, loam, clay) and drainage patterns of the planting site is an important first step in choosing appropriate plants. A discussion on the physical habitat characteristics for prairie types can be found in Curtis (1959).

Common to all prairie sites is full exposure to the sun. A rule of thumb that can be used to ensure sufficient light is to have an enclosure with no more than a 1:1 height to width ratio. That is, if 20 feet is the narrowest part of the planting area, no enclosure elements on the east, west, and south such as fences, trees, etc. should be more than 20 feet in height.

Prairie Community Structure

Any prairie has the potential to contain hundreds of species which are adapted to its physical conditions, but not all possible species occur on any single site. This can be attributed to many circumstances including site history, seed source proximity, competitive species interactions, and chance. Current ecological theory does not provide a model for duplicating all of the functions and dynamics of a natural prairie; however, by emulating part of the physical and temporal structure of these communities, some of these features can be created. Of particular significance are: (1) the relative importance of different taxonomic groups; (2) the differentiation between common and rare species; (3) the seasonal sequence of growth and blooms; and (4) the relationships between prairies and other plant communities.

By definition, the prairie is dominated by grasses (Curtis 1959) which often occupy over 90% of the prairie vegetation cover (Morrison 1981). This dominance of grass cover over that of prairie forbs does not extend to species numbers. In Wisconsin prairies, for example, the proportion of species belonging to the Poaceae (grass family) ranges from 13.7% in dry prairies, to 8.1% in wet-mesic prairies (Curtis 1959). Eighty percent of the species may be classified as forbs. The remaining species consist of trees and shrubs. Although grasses predominate throughout a prairie stand, there is often great variation in the proportion of grasses to forbs from one location to the next. Within natural prairies localized percentages of grass cover may range from 90 to 10 with the remaining cover contributed by forbs, trees, and shrubs. The proportion of grasses to forbs is an important determinant of a prairie's visual effect. The variability of this ratio in natural models allows room for individual interpretation. To meet the botanical definition of this community type, it is perhaps best to stay within a range of 50% to 90% grass cover. However, for aesthetic purposes, such as a desire for many colorful flowers and fruits, a greater percentage of forbs may be used in selected locations. A high percentage of forbs throughout a prairie planting is not advised. Grasses tend to be a visual unifier in terms of color, texture, and form. They serve as a visual backdrop to the forbs and as a structural support for many of the tall flowering species.

In addition to the Poaceae, taxonomic families important to Wisconsin prairie, either because of numbers of species or abundance of plants include the composites (Asteraceae), the legumes (Fabaceae), roses (Rosaceae), milkweeds (Asclepiadaceae) and mints (Labiatae) (Curtis 1959). To the extent that taxonomic designations reflect genetic and ecological information, the inclusion of appropriate species from these families improves the natural functions of the plantings.

As is true of most natural communities, prairies contain a few species which are relatively common and a larger number of species which are relatively rare. Common species are usually abundant at any given site and also are found in a wide range of prairie sites. Examples are *Andropogon gerardi* and *A. scoparius* (*Schizachyrium scoparium*) big and little bluestem grasses. Relatively rare species include *Monarda fistulosa*, wild bergamot, found on a wide range of sites but in relatively low numbers, and those restricted by habitat such as *Cypripedium candidum*, small white lady's-slipper orchid, a species of calcareous wet prairies, bogs, and fens. Prairie plantings, then, should include species present in different proportions, a few which are abundant, and many which are relatively uncommon.

Prairies, relative to many other natural communities in the midwest, provide a continuing profusion of flowers. One or another species is in bloom from early spring to late fall. Prairie types differ in the way their blooms are apportioned throughout the year. For example, in Wisconsin, dry prairies have their greatest show of flowers in spring and fall, the mesic and wet prairies from mid to late summer (Curtis 1959).

Prairie constituents can be distinguished as cool-season or warm-season species. Cool-season plants are species such as *Bromus kalmii*, prairie brome, which grow actively in early spring, become dormant during the hot weather of mid-summer and become active again in autumn (Risser et al. 1981). Warm season species start development later in the year, reach a peak of activity in mid to late summer, and become dormant in early autumn (Risser et al. 1981); *Andropogon gerardi* and *Sorghastrum nutans*, Indiangrass, are examples (Waller and Lewis 1979). Depending on the prairie, different proportions of these types of species prevail. In a planting, species which represent the appropriate blooming seasons and growth patterns can enhance the dynamics and functioning of the community.

Prairies have many species in common with other plant communities. For example, savannas are described as a combination of grassland and forest in which the majority of the land is occupied by prairie grasses and forbs but has a scattering of trees (Curtis 1959). Forests may contain species such as *Dodecatheon meadia*, shooting star, *Amorpha canescens*, leadplant, and *Andropogon scoparius*, which are generally found in prairies (Holtz and Howell 1983). These relationships can be expressed spatially, as a rolling prairie gradually blends into a wooded hillside or through time, as when a prairie becomes invaded by brush and then by trees. A designer can take advantage of these transitions to create continuity on a site consisting of a variety of community types (Diekelmann and Schuster 1982).

Design Elements

The patterns formed by the colors, textures, forms, and lines of the species that comprise the prairie community are important components of its aesthetic character. These patterns are largely due to species placement, which in turn is governed by microclimate variations, plant reproductive characteristics and species interactions. Some species form tight clumps, others appear to be scattered throughout an area. Placement of specific plants or seeds in a design setting should mimic the natural distribution patterns of the species. The distribution pattern must relate to physical site characteristics. For example, drifts of prairie smoke (*Geum triflorum*) can be placed along dry south-facing slopes.

Color patterns are extremely important visually. Overall, the prairie is dominated by foliage color and particularly by the relatively fine textured grasses which when viewed from a distance create a wash of background color. Drifts or patches of flowering forbs create variety and contrast viewed against this background. Vivid and vibrant color combinations occur when the orange flowers of *Lilium michiganense*, Turk's cap lily, stand out against the grass greens or when *Echinacea pallida*, pale purple coneflower, grows in close proximity to *Asclepias tuberosa*, butterfly milkweed. More relaxed and soothing effects are created when cool colors such as blues and greens occur together or when tint or shade contrasts appear within one hue. For example, consider the blue violet flowers of asters and gentians against green foliage or the dark greens of rushes against the bright green of *Spartina pectinata*, cord grass. As might be expected from the blooming sequence of prairie communities, as well as the seasonal pattern of growth and decline, the color patterns change throughout the year. Foliage ranges from the greens of spring and summer to the reds and browns of fall and winter. Early spring flowers are white and pink and lemon yellow; fall blooms are deep purple and golden yellow.

Varying forms and textures are also important to the prairie's visual effects. Of particular interest is the overall form of natural prairie stands. Prairies are often thought to be expansive and open, a land that continues outward to the skyline. The rolling topography

TABLE 1. Plants that require special consideration in natural landscapes.

Species	Characteristics*
Anemone canadensis (Canada windflower)	2, 1, 4
Apocynum androsaemifolium (spreading dogbane)	2, 3
Apocynum cannabinum (Indian hemp)	2, 3
Aquilegia canadensis (columbine)	1, 3
Aster laevis (smooth blue aster)	1, 3, 5
Aster novae-angliae (New England aster)	1, 4, 5
Coreopsis palmata (prairie coreopsis)	2, 4
Coreposis tripteris (tall coreopsis)	2, 4, 5
Elymus canadensis (canada wild rye)	1, 3, 5
Fragaria virginiana (wild strawberry)	2, 4
Helianthus spp. (sunflowers)	2, 4, 5
Panicum virgatum (switchgrass)	2, 4
Penstemon digitalis (smooth beardtongue)	1, 3
Potentilla simplex (old field cinquefoil)	2, 3
Ratibida pinnata (yellow coneflower)	1, 3, 5
Rosa spp. (roses)	2, 3
Smilacina stellata (starry false Solomon's seal)	2, 3
Solidago altissima (tall goldenrod)	2, 3
Solidago canadensis (Canada goldenrod)	2, 3
Solidago rigida (stiff goldenrod)	1, 2, 4
Sorghastrum nutans (Indiangrass)	1, 3, 5
Spartina pectinata (cordgrass)	2, 4
Zizea aurea (golden Alexanders)	2, 3, 5

*Key: 1 - self-sows rapidly, 2 - spreads rapidly by vegetative means, 3 - does not appear to adversely affect neighboring plants and can be included to help suppress weeds, 4 - thought to adversely affect neighboring plants on occasion, 5 - tends to grow large and floppy in garden situations.

of southern Wisconsin and northern Illinois begins to provide a sense of enclosure. The sense of enclosure can also vary seasonally as the prairie plants change in height from a few centimeters to several meters tall. What appears to be a vast open plain in spring becomes a dense wall of vegetation in late summer.

The forms and textures of individuals or small groups of plants also create interest as they stand out against the grassy background. These forms and textures can be observed to change through the season. For example, in early summer, the forms of *Baptisia leucantha*, white false indigo, can appear as miniaturized oak trees marching through the prairie. The glossy, sun-reflecting leaves of *Spartina pectinata* contrast significantly with the duller leaves of *Andropogon gerardi* in mid summer. In the fall, the soft, fine-textured cottony seedheads of *Andropogon scoparius* sparkle as the plants drift among many medium and coarse textured forbs and taller grasses. Contrasts of form, texture, and color can also be very striking, especially if they are found sparingly. A lone *Asclepias tuberosa* or *Silphium terebinthinaceum*, prairie dock, placed amidst fine-textured grasses creates a strong impact in a small space. A phenological chart, listing prairie species and their local dates for appearance, blooming and fruiting, can be useful when selecting and juxtapositioning species in a planting. Careful selection can assure interest in form, color and texture throughout the year.

Desired Planting Characteristics

Most residential prairie plantings are on sites much smaller than the vast tallgrass prairie, and many are smaller than even the natural limestone hill prairies of the midwest. Careful selection and placement of species, however, can create an expansive feeling even in small front or back yards.

Vegetative enclosure, if needed, can be one of a dynamic to smoothly curved irregular appearance. This reflects and symbolizes the dynamic qualities of the prairie. If room allows, trees and shrubs in islands or promontories can be placed so that the end of the space cannot be seen, thus making the view seem larger.

Choosing predominantly fine-textured and short grass species such as *Andropogon scoparius* and *Bouteloua curtipendula*, side oats grama grass, and forbs such as *Petalostemum candidum* white prairie clover, and *Phlox pilosa*, prairie phlox, also contribute. These short species provide less of an enclosure than do taller plants. When viewed from only a short distance, the fine-textured species lose their individuality and merge into a unit. One visual cue we use to judge distance is the loss of individual detail; fine-textured species provide this cue at a shorter distance than do more coarse-textured plants and thus contribute to a feeling of spaciousness.

If fine-textured species are used to form the majority of the planting, coarse-textured plants such as *Heliopsis helianthoides*, false sunflower, can be used sparingly to create visual contrasts. A few coarse-textured plants in the foreground increase the illusion of depth even more. By placing such accent plants at irregular intervals or in drifts loosely parallel with the axis of the planting, they can lead the eye through the prairie, again creating a fluid, dynamic, expansive feeling.

Residential plantings usually include walkways to allow access to the prairie. These can be mowed paths covered with turf grass; or, in fertile soils where invasion of turf grass into the plantings is a problem, they can be paved with a solid material such as flagstone. As prairie plantings in a residential site will often grow taller than in natural conditions, they will often fall over and obstruct the walkways. For this reason it is best to place plants that might fall at a distance from the edge of the planted area equal to their expected height.

Other important factors are the growth rate and relative aggressiveness of different plants. Some species such as *Aster novae-angliae*, New England aster, or *Coreopsis palmata*, prairie coreopsis, spread rapidly, especially in a newly established planting. If such plants are desired, they should either be established in small numbers or not included until the majority of the planting is under way (Table 1).

PROTOTYPICAL PLANTING

In order to illustrate how this general approach might apply to a residential planting, consider the following prototype for an average suburban site. Table 2 provides a summary of the major criteria for selecting an appropriate prairie type for the site and for choosing species and their proportions. The site is assumed to be flat with well-drained loam soil and full sunlight. These characteristics suggest that a dry-mesic prairie is appropriate (Curtis 1959).

This example assumes the use of all started plants rather than seeds. This choice will eliminate some of the weed problems which may occur in seeded plantings and which may cause adverse reactions from neighbors.

TABLE 2. Criteria influencing the selection of prairie type and species composition.

General Criterion	Site Condition of Example
Topography	Flat
Drainage	Well-drained
Soil texture	Loam
Decision: Dry-Mesic Prairie	

Determination of Species and Proportions:	
General Criterion	Site-Specific Decision
Grass-forb ratio	50:50
Families	*Include representatives of composite, grass, legume, rose, milkweed families.
Blooming times	*1/4 to bloom in spring, 1/2 in summer, 1/4 in fall.
Species proportions	*More forb than grass species. Emphasize fine textured species. Emphasize short species. Few rapid growing, aggressive species.

*Characteristics of Wisconsin dry-mesic prairies (Curtis 1959).

TABLE 3. Prairie prototype plant list with forbs and shrubs grouped According to blooming periods.

43 FORBS: Approximately 1/4 blooming in the spring, 1/2 blooming in the summer and 1/4 blooming in the fall. Forbs are listed by their approximate blooming dates (based on observations and information in Swink and Wilhelm 1979).

Spring (May-Late June)

Geum triflorum (prairie smoke)
Sisyrinchium campestre (blue-eyed grass)
Viola pedatifida (prairie violet)
Dodecatheon meadia (shooting star)
Hypoxis hirsuta (yellow-star grass)
Zizea aptera (heart leaved meadow parsnip)
Galium boreale (northern bedstraw)
Phlox pilosa (prairie phlox)
Tradescantia ohiensis (spiderwort)
Rosa carolina (carolina rose)
Baptisia leucophaea (cream false indigo)
Baptisia leucantha (white false indigo)

Summer (Late June-Middle August)

Blephilia ciliata (Ohio horsemint)
Echinacea pallida (pale purple coneflower)
Euphorbia corollata (flowering spurge)
Petalostemum candidum (white prairie clover)
Rudbeckia hirta (brown-eyed susan)
Asclepias tuberosa (butterfly milkweed)
Coreopsis palmata (prairie coreopsis)
Heliopsis helianthoides (false sunflower)
Amorpha canescens (lead plant)
Ceanothus americanus (New Jersey tea)
Parthenium integrifolium (wild quinine)
Allium cernuum (nodding wild onion)
Cacalia atriplicifolia (pale indian plantain)
Helianthus occidentalis (western sunflower)
Pycnanthemum virginianum (mountain mint)
Ratibida pinnata (yellow coneflower)
Silphium laciniatum (compass plant)
Veronicastrum virginicum (Culver's root)
Eryngium yuccifolium (rattlesnake master)
Silphium terebinthinaceum (prairie dock)
Petalostemum purpureum (purple prairie clover)

Fall (Late August-October)

Helianthus laetiflorus (prairie sunflower)
Liatris aspera (blazing star)
Solidago rigida (stiff goldenrod)
Aster laevis (smooth blue aster)
Aster novae-angliae (New England aster)
Aster azureus (sky blue aster)
Gentiana puberula (downy gentian)
Prenanthes racemosa (glaucous white lettuce)
Solidago speciosa (showy goldenrod)
Aster oblongifolius (aromatic aster)

GRASSES

Andropogon gerardi (big bluestem)
Schizachryium scoparium (little bluestem)
Bouteloua curtipendula (side oats grama)
Sorghastrum nutans (Indian grass)
Sporobolus heterolepis (prairie dropseed)

Forty-eight species, consisting of forty-three forbs and five grasses are included in the planting (Table 3). The forbs were chosen to have at least two species in bloom each week of the growing season and to reflect the blooming sequence of dry-mesic prairies; 1/4 of all species bloom in the spring, 1/2 in summer, and 1/4 in fall (Curtis 1959). In Madison, Wisconsin,there are approximately 22 weeks in the growing season, which influences the numbers used. Forty-eight species is in the range of species densities for Wisconsin prairies presented by Curtis (1959) and probably represents the lower range of the number of species found in small prairie remnants. Most of the plants are readily available from nurseries and/or are easily grown from seed. The majority are fine-textured, and relatively small in keeping with the scale of the site. Some larger plants, or those which are particularly showy or have distinctive textures, are also included for accents.

Once the species to be included are chosen, the next step is to determine their proportions. Table 4 illustrates our approach which involves an initial classification of species in terms of both their visual and their physical and behavioral characteristics. In this example, the forbs are divided into three groups, the grasses into two. Fewer individuals are planted in the large-sized or aggressive groups than in the smaller-sized less-aggressive ones.

Several trade-offs are involved in the decision as to actual numbers. Cost and availability of plants and the time needed to develop into an established community are considerations. Table 5 lists a basic planting scheme for a hypothetical 400 ft² (37 m²) plot and two alternatives which differ in the total number of plants installed.

The basic planting includes 400 plants at a density of one plant per square foot (approximately 30.5 cm between plants). The mix has 200 forb plants and 200 grass plants. Alternative I includes 600 plants and involves an increase in the density of the forb plants. Alternative II involves 800 plants installed at twice the density of that of the basic planting. The relative proportions of the different forb groups and of the grasses remains the same for all three

TABLE 4. Criteria for relative numbers of species.

FORBS

Name	Characteristics
Group 1. Large sized, spreads rapidly, and/or self-sows rapidly.	
Aster novae-angliae	large, self-sows rapidly
Baptisia leucantha	large
Cacalia atriplicifolia	large
Coreopsis palmata	spreads rapidly
Helianthus laetiflorus	spreads rapidly, large
Helianthus occidentalis	spreads rapidly
Heliopsis helianthoides	large
Parthenium integrifolium	large
Ratibida pinnata	large, self-sows rapidly
Silphium laciniatum	large
Silphium terebinthinaceum	large
Solidago rigida	large, self-sows rapidly
Veronicastrum virginicum	large
Group 2. Medium sized and/or showy.	
Asclepias tuberosa	Showy
Ceanothus americanus	Showy
Eryngium yuccifolium	Medium
Group 3. Species remaining (see Table 3).	

Grasses

Group 1. Large sized	Group 2. Medium sized
Andropogon gerardi	Schizachryium scoparium
Sorghastrum nutans	Bouteloua curtipendula
	Sporobolus heterolepis

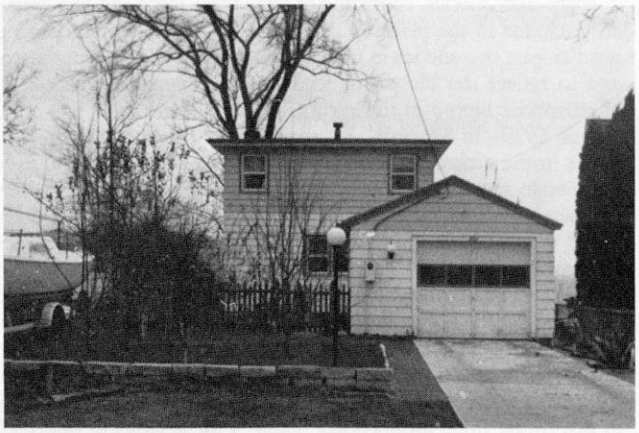

FIG. 1. View of example site prior to planting.

FIG. 2. Same view of example site after the plantings have become established.

schemes. Eighty-one percent of the forb plants are classified as fine-textured, and relatively unaggressive. Ninety percent of the grasses are medium-sized and/or fine-textured. In general, Alternative II results in the most natural-appearing and the most rapidly established planting. It is also the most expensive to implement due to the large number of plants to purchase and the increased labor necessary to install and maintain them to an established state.

EXAMPLE RESIDENTIAL PLANTING

To best illustrate our approach to residential landscaping with prairie, it is helpful to describe an actual residential site designed with these principles in mind.

The site illustrated in Fig. 1 is a long narrow lot (10.2 m x 62.2 m) in Madison, Wisconsin. The north lot line is bordered by a street, the south by a large lake. Neighboring residences are found to the east and west.

Before the planting the street entrance was visually dominated by a long expanse of concrete driveway. A variety of existing shade patterns were cast by buildings and trees on and off of the site which indicated where prairie and woodland plantings would be appropriate. Privacy and design considerations were important in determining where any shrub border and herbaceous edge plantings were to go (Diekelmann and Schuster 1982). Plant species were selected to reflect and symbolize indigenous plant community composition.

In the planting the arrangement and use of design elements

TABLE 5. Example plot.

400 Square Feet ($37m^2$)

BASIC PLANTING
1 plant per sq. ft. (12 inches (30.48 cm) between species.

400 Plants

200 forb plants*	200 grass plants*
26 Group 1 (2 ea. of 13 species)	180 Group 1 (60 ea. of 3 species)
12 Group 2 (4 ea. of 3 species)	20 Group 2 (10 ea. of 2 species)
162 Group 3 (6 ea. of 27 species)	

Comments: Least expensive, clumpy appearance, tall plants may fall over. Advisable to wait 3 growing seasons before planting rapid spreaders and self-sowers.

ALTERNATIVE I
2 forb plants per sq. ft., one grass plant per sq. ft.

600 Plants

400 forb plants	200 grass plants
52 Group 1 (4 ea. of 13 species)	180 Group 1 (60 ea. of 3 species)
24 Group 2 (8 ea. of 3 species)	20 Group 2 (10 ea. of 2 species)
324 Group 3 (12 ea. of 27 species)	

Comments: More expensive, less clumpy appearance than above. Advisable to wait 2-3 growing seasons before planting spreaders and self-sowers.

ALTERNATIVE II
2 plants per sq. ft. (grasses and forbs)

800 Plants

400 forb plants	400 grass plants
52 Group 1 (4 ea. of 13 species)	360 Group 1 (120 ea. of 3 species)
24 Group 2 (8 ea. of 3 species)	40 Group 2 (20 ea. of 2 species)

Comments: Most expensive; however, gives most natural appearance of three alternatives. Rapid spreaders and self-sowers may be planted immediately.

*See Tables 3 and 4 for species.

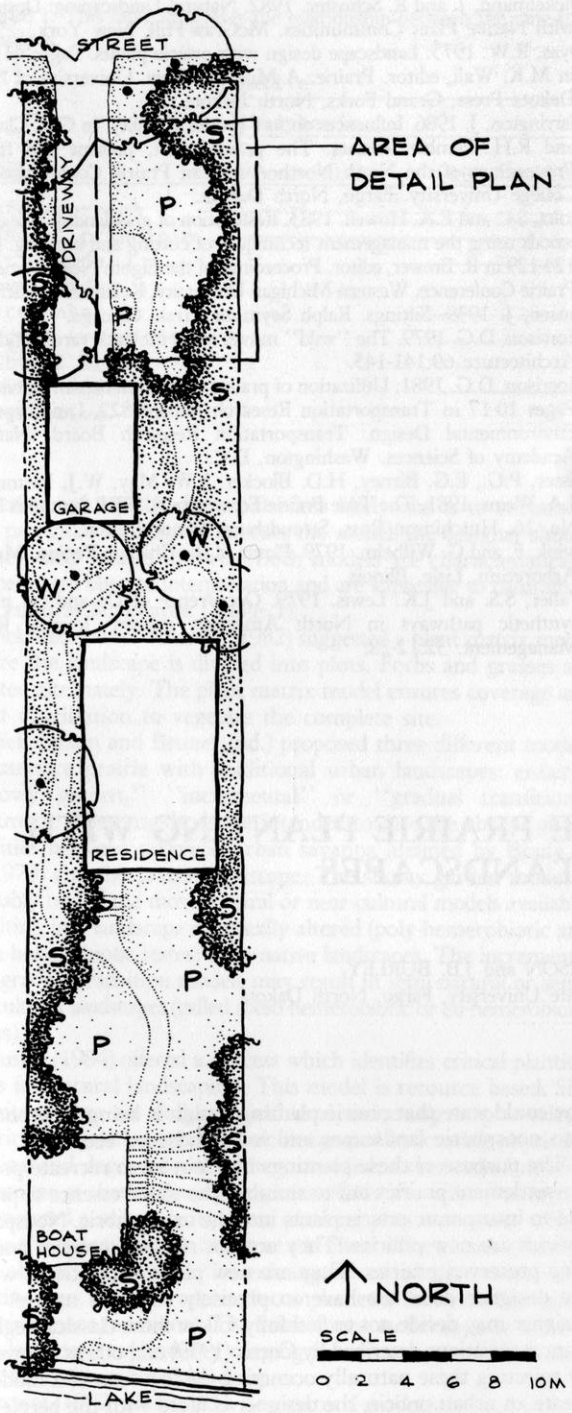

FIG. 3. Example site's overall landscaping plan.

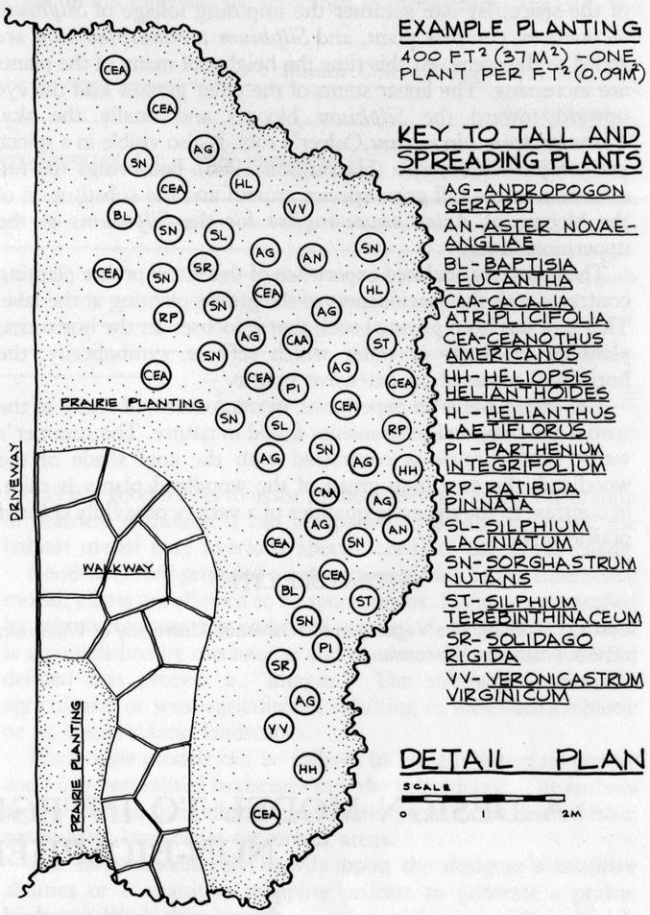

FIG. 4. Example site's detailed prairie planting plan.

such as light, color, texture and spatial enclosures moderate the long narrow character of the site and complement the view of the lake. A series of spaces exist, both open to the sky and shaded. Plantings have broken up the space by strategically blocking some views and enhancing others. In doing so the extreme linear character of the site has been modified. The entrance drive is softened by light and shade patterns created by adjacent trees, which cut down the glare emanating from the driveway (Figs. 2 and 3) and add a dynamic quality to the ground as the sun moves across the sky (Jensen 1939).

The prairie planting opposite the entry drive is small and enclosed, and reflects many of the small prairie openings found in the midwest. This planting consists of the species listed in Table 3. The detail plan (Fig. 4) shows the locations of the spreading and/or tall plants, which are, and will be, a relatively conspicuous part of the planting. The taller species are concentrated near the eastern edge of the site away from walks which they might obstruct.

Two major visual rhythms which vary throughout the growing season are formed by taller species. The first visual rhythm consists of horizontal repetition of form and color along the drive, directing the view along the entry space towards the house. In early summer the mounded white blooms of *Ceanothus americanus,* New Jersey tea, fulfill this role. Other relatively coarse-textured plants such as *Baptisia leucantha, Heliopsis helianthoides* and *Parthenium integrifolium,* wild quinine, contrast with the relatively fine textures of the rest of the planting and are used as repetitive visual elements.

The second visual rhythm is the use of the vertical feeling of the taller plants which, as they grow, tend to lead the eye upward,

encouraging the viewer to make the sky part of the experience of the space. By late summer the imposing foliage of *Silphium laciniatum*, compass plant, and *Silphium terebinthinacium* are added to the scene. At this time the heights of many of the plants are increasing. The linear stems of the taller grasses lead the eye upward toward the *Silphium* blooms and finally the sky. *Veronicastrum virginicum*,Culver's root, is also visible in a minor yet complementary role (Harrington 1986). Fall brings the full extension of the tall grass species growth and the substitution of the blooms of *Aster novae-angliae* for the *Silphiums* at the uppermost layer.

The relatively enclosed experience of this small prairie planting contrasts with the spaciousness of the prairie planting at the lake. This area has been planned such that it focuses on the horizontal plane of the body of water which reflects, symbolically, the horizontal plane of an extensive prairie.

The entire site is an experience, in microcosm, of many of the spatial and temporal relationships found in nature. The summer's warm sunlit prairie is contrasted with the cool shade of the woodland; the cool blue green of the woodland plants is calm, in contrast to the dynamic qualities of a variety of vividly colored prairie flowers.

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A DESIGN MODEL TO INTEGRATE PRAIRIE PLANTING WITH NON-BIOSPHERIC LANDSCAPES

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Abstract. Minnesota prairie vegetation shapes and patterns were examined at various landscape scales to generate a design model for man-made prairie landscapes. The model describes the distribution of vegetation shapes to be incorporated into the landscape. Vegetation shapes significantly concur ($p < 0.1$) between different landscape scale classes. The model notes the number of protrusions, indentations and holes each shape is likely to contain. The pattern within a given area is also described. Small scale patterns are significantly different ($p < 0.01$) from regional patterns. A five step process is presented to visually create the essence of prairie under the most geometric and cultivated landscape conditions. Methods to manage the edges of the man-made cultivated prairies are discussed.

INTRODUCTION

Nature has traditionally been a major inspirational resource for the generation of urban landscape design. Over the last fifty-five years, native prairie landscapes have become a recognized and legitimate inspirational resource in the creation of urban form. Dyas (1975) documented several examples where prairie vegetation has been incorporated into urban landscape and where humans were involved in selective and controlled use of prairie planting patterns for cities. Controlled landscapes are termed "noospheric" (Vernadsky 1945). Noospheric landscapes, which are drastically controlled by man (Bakker 1979), contain few naturally occurring species and many newly introduced species (van der Maarel 1975). Naveh and Lieberman (1984) define studying noospheric vegetation patterns as part of a discipline termed "landscape ecology." Thus one could state that prairie planting design is being incorporated into noospheric landscapes and into landscape ecology.

The purpose of these plantings may not be to recreate precise pre-settlement prairies but to simulate the visual essence of prairie and to incorporate prairie plants into the urban fabric. Noospheric prairies are new prairies. They are not restored prairies nor are they preserved prairies. They are new plant associations, where the designer does not have to precisely replicate nature. The designer may decide not to faithfully follow those classical regional plant associations described by Curtis (1959) and others. However, by rejecting these naturally occurring descriptions as a model to create an urban prairie, the designer is faced with the perplexing situation of "what description (model), if any, to follow?" In urban landscapes there are few precedents to determine the appropriate prairie planting palette, appropriate planting scale, appropriate vegetation configurations or appropriate prairie interface with other urban landscapes.

Several notable landscape architects and designers have generated models for noospheric prairie. Morrison (1980) suggested two models in the creation of prairie landscapes. The first is the vista model. When viewing prairies on a large scale, prairies become a sea with weaving bands of plant materials interwoven across the landscape. When using this model the designer should attempt to create these weaving bands of plant material and create a mosaic pattern across the landscape. The second is termed the adjacent model. This model is applicable to most forb species. It states that forbs are clustered. This means that the farther one recedes from

TABLE 1. This table illustrates the relationship between the nine models described in this paper and the application to various native and cultivated landscapes.

	Native ← Human Controlled/Cultivated →				
	Biospheric ← Noospheric →				
MODEL	A-hemerobiotic	Oligo-hemerobiotic	Meso-hemerobiotic	Poly-hemerobiotic	Meta-hemerobiotic
Vista approach	----------	----------	----------	----------	----------
Adjacent principle	----------	----------	----------	----------	----------
Matrix model		----------	----------	----------	----------
Showy garden				----------	----------
Incremental		----------	----------	----------	
Gradual transition		----------	----------	----------	
Critical area		----------	----------	----------	----------
Habitat model		----------	----------		
Subtractive				----------	----------

the center of a plant cluster, the less likely one is to encounter that particular species. To execute the model, the designer should cluster each species of forbs. Both models are characteristically aesthetic, are open to interpretation and are applicable to naturalistic and cultural landscapes (Table 1).

Diekelmann and Schuster (1982) suggested a plant matrix model where the landscape is divided into plots. Forbs and grasses are planted alternately. The plant matrix model ensures coverage and plant distribution to vegetate the complete site.

Diekelmann and Bruner (nd.) proposed three different models to interface prairie with traditional urban landscapes: either a "showy garden," "incremental" or "gradual transition" treatment. These methods are intended to ease the abrupt visual qualities between a typical urban savanna (defined by Brady et al. 1979) and the prairie landscape. The showy garden model is probably one of the most cultural or near cultural models available, resulting in a landscape drastically altered (poly-hemerobiotic and meta-hemerobiotic states) from native landscapes. The incremental and gradual transition models may result in semi-natural or semi-agricultural landscapes (called meso-hemerobiotic or eu-hemerobiotic states).

Austin (1984) offered a process which identifies critical planting areas for natural landscaping. This model is resource based. Site inventory data are collected and analyzed using map overlays. Priority revegetation locations are designated by locating physically eroding and degraded sites. Plant material is then scheduled for placement at these priority locations. After the critical area plan is generated a subsequent phased planting plan is prepared which meets the specific design intent of the client. The phased planting plan should blend with the existing forms of the critical area planting plan. Austin's approach complements the aesthetic models by being more functional. The critical area model appears to have wide landscape applicability ranging from near-natural landscapes to completely cultural landscapes.

Smyser (1982) illustrated a near-natural model where plants are located according to the site's ecological potential. While every model may examine vegetation potential, this model is ecologically comprehensive. The program for placing vegetation is based primarily upon the land's ability to support specific prairie vegetation. Programs from other models often incorporate a client's needs into vegetation locations. In the model described by Smyser, the selection of vegetation is performed only after a detailed site inventory is completed and a complete ecological analysis is conducted. A plant suitability habitat map is then created which delineates the potential location of various plant associations. This model generates vegetation patterns based upon the site's intrinsic physiography. This model is probably the most biospheric sympathetic. Smyser used this process to create landscapes which are in the near natural state (a-hemerobiotic or oligo-hemerobiotic states). This model is termed the "habitat model." The habitat model is a good model to assist in the preservation and restoration of prairies. Although it can be applied to urban situations, the habitat model may overlook special needs of the urban client.

Kenfield (1966) provided a subtractive model. In the subtractive model, plants are allowed to be spontaneous. Plants are controlled by selectively removing undesired vegetation. Vegetation removal is accomplished by mechanical and chemical treatments. Kenfield defined this process a "intagio." The subtractive model is agricultural or semi-agricultural, resulting in meso-hemerobiotic or eu-hemerobiotic landscapes.

These nine models can be utilized to visually integrate prairie and other naturalized landscapes into the urban fabric. The authors are pioneers in their efforts to delineate spatial forms derived from naturalistic landscapes for urban areas.

The nine models rely heavily upon the designer's intuitive abilities or a cognitive mapping process to generate a prairie landscape. While these models are very useful, many of these models lack an investigative empirical base to provide a theoretical form-giving concept in the creation of urban prairies. Therefore a new model was sought which attempted to extract the visual essence of native prairie vegetation patterns and quantitatively describe the physical configurations of prairie.

The problem statement for the new model was: "Did there exist a native Minnesota prairie planting pattern or configuration that could be mathematically identified and applied to noospheric prairies?" To examine this statement, four subproblems were identified:

1. Are there previous or potential mathematical measures to describe plant distributions and vegetation patterns? If yes, what other features might be measured? If not, what features concerning shape could be measured?
2. Are there existing historical prairie records or existing prairies that could be descriptively measured for shape and configuration?
3. Upon measuring these prairies, were there any discernible and identifiable descriptive patterns emerging from the data set?
4. Could these identifiable features be abstracted and applied to noospheric prairies?

Several notable constraints arise concerning these four subproblems. First, plant distribution has traditionally been studied in some mathematical detail; however the study of iconic landscape shapes and patterns has been limited to mathematical representations including frequency, density and dominance which may indicate uniform, clustered or regular vegetation patterns. The actual configuration of the shape and pattern has not been extensively studied. This means that there are probably limited methods to assess shape and pattern plus limited examples to follow as guidelines for generating quantitative visual images.

Second, information generated from a map also has severe categorical and cartographic limitations (Anderson 1980). Generalized categorical maps and generalized cartographic maps will have a tendency to contain simple shapes and simple patterns. Thus the map and its contents have a tendency to bias the shape and pattern information.

Third, mapping scale is an important feature to consider. Different mapping scales contain different classes of information. For this study, land units and mapping classes were established in relationship to current anthropocentric standards in landscape design. These categories are not absolute; instead, these categories relate to how humans design landscapes on paper, the size of paper humans use, the types of marking devices humans use to design landscapes and the resolution humans are able to perceive. In nature, these categories may be completely arbitrary and have no empirical basis; yet for human purposes, these categories can have meaning and may be useful. The mapping scales are divided into the following categories:

1. Microchore (small scale distribution patterns): From a traditional landscaping perspective, the microchore is an extremely small landscape parcel ranging in size from 0.1 to 2 meters or about the size of a dish garden or very small planter. The mapping of most horticulturally grown herbaceous species (hemicryptophytes and cryptophytes) is easily accomplished at this scale. The representative fraction is typically 1:1. The map scale is 1 cm = 0.01 m.
2. Mesochore (intermediate scale distribution patterns): This landscape is about the size of a small yard, approximately an area 10 m x 10 m. The representative fraction is typically 1:100. The map scale is 1 cm = 1 m. At this scale most woody plants (phanerophytes and chamaephytes) are easily mapped and located. Some hemicryptophytes and cryptophytes are too small and detailed to map and can be described only as mass plantings. This scale is useful for detailed site design.
3. Macrochore (large scale distribution patterns): This landscape is about the size of a small park or 100 m x 100 m and slightly larger. The representative fraction is approximately 1:10,000. The scale for mapping is typically 1 cm = 100 m = 0.1 km. Clusters and associations of phanerophytes and other plants (termed by some authors as plant communities or landscape units) can be easily mapped. This scale typically is useful for large scale site planning.
4. Polychore (many patterns and distributions): This landscape is about the size of the difficult-to-define and often ambiguous, but important "region" and is useful for regional and state planning. The representative fraction is approximately 1:1,000,000. The scale is 1 cm = 10,000 m = 10 km. This mapping scale is useful to map associations of associations (called by some biomes or land systems).

With these constraints and limitations, the study team examined current measuring methods and developed procedures for this study.

METHODS AND MATERIALS

While there are limited measures to describe shape and pattern, two appeared suitable. The first is the shape diversity index "Ds" suggested by Patton (1975):

$$Ds = \frac{P}{2\sqrt{\pi A}}$$

Ds = Shape Diversity Index
P = Perimeter
A = Area
π = 3.14

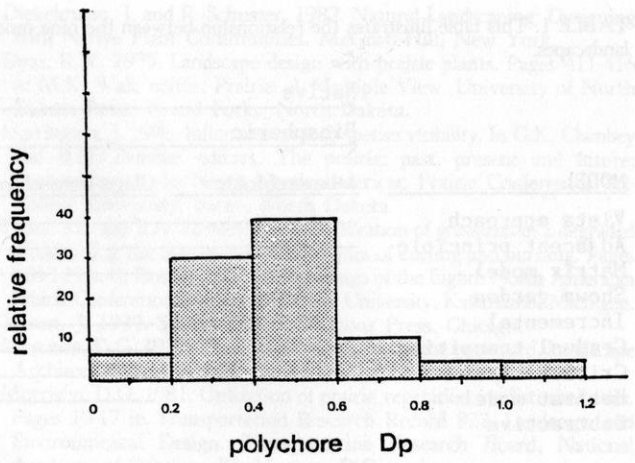

FIG. 1. Polychore patterns are relatively simple with a small variance.

This was used to describe the shape diversity of plant distributions. A perfect circle will result in a shape diversity score of 1. Long snake-like shapes will have scores near 2. Highly intricate shapes may have scores greater than 3. Intricate shapes often have physical features such as indentations, protrusions and holes associated with the shape.

The second measure is pattern diversity, "Dp." An area is examined by measuring the edges of shapes contained within the specified area.

$$Dp = P/A$$

Dp = Pattern Diversity Index
P = Perimeter
A = Area

This measure does not consider the perimeter of the area as part of the edge (Thomas et al. 1979). The measure is a modification of the index suggested by Patton. A uniform landscape will result in a pattern diversity score of 0. Highly intricate patterns with many vegetative associations can score greater than 10.

There is limited historical information concerning prairie shapes and patterns available for measurement. The historical data consisted of maps (Barnard 1980) illustrating large site (macrochore) vegetation patterns and maps (Marschner 1974) illustrating regional (polychore) vegetation patterns and shapes. To complement the macrochore and polychore information, the study team gathered field observations of shape distributions for individual species. The field observations consisted of photographs and field notes concerning the configurations of plant species in Minnesota prairies. The mass configurations of each plant species can be considered the mesochore information class. No microchore information was gathered.

Mesochore shapes (n = 56) were measured from field maps by determining the area of the configuration in square feet and the perimeter of the configuration in lineal feet. The number of holes, intrusions and protrusions were also noted for each configuration. The configuration was computed using the first equation.

Polychore shapes (n = 68) were measured by randomly selecting vegetation configurations on the Marschner (1974) map, determining the area of the configuration in square miles and determining the perimeter of the configuration in lineal miles. The diversity index was computed using equation one. The number of indentations, protrusions, and holes were also recorded for each configuration.

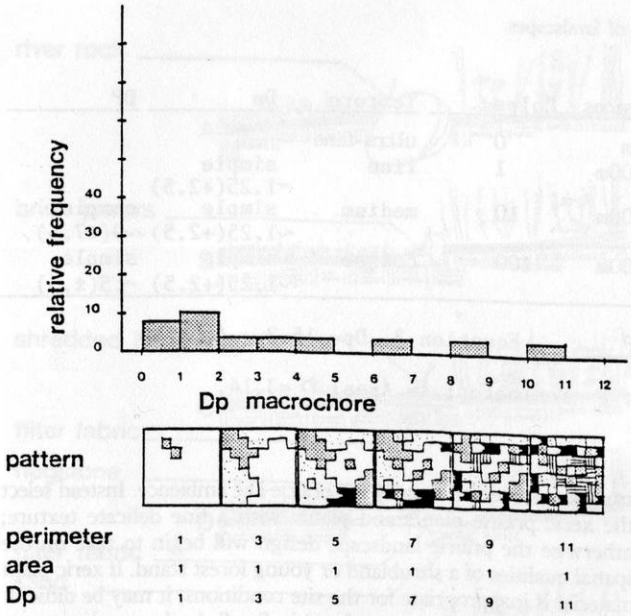

FIG. 2. Notice the relatively large variance in macrochore patterns.

Macrochore patterns (n = 27) were measured on the Barnard (1980) map by determining the area of the map in square miles and determining lineal miles of interior edges. The pattern of the area was computed using the second equation.

Polychore patterns (n = 30) were measured by randomly selecting plots three-hundred forty-two square miles in area and measuring the lineal miles of interior edges. The pattern of the area was computed using equation two.

Mesochore and polychore shape diversity index (Ds - derived from the first equation), plus indentation means, protrusion means and hole means were compared in "Epistat" (Gustafson nd.). Macrochore and polychore pattern diversity index (Dp -derived from the second equation) were compared using non-parametric statistical methods.

RESULTS

The distribution of the pattern diversity index scores, "Dp," approximated a normal distribution, allowing parametric statistical procedures. There was a significant difference ($p < 0.01$) between the macrochore pattern diversity index mean and the polychore pattern diversity index mean. The estimate of the mean polychore pattern was 0.46. A score of 0.46 indicates a relatively uniform pattern with occasional disruptions in uniformity. The distribution of the polychore pattern is illustrated in Fig. 1. The estimate of the macrochore pattern diversity was 15.4. A score of 15.4 indicates a complex pattern with no indication of uniformity. The distribution of the macrochore pattern is illustrated in Fig. 2. A regression line was constructed for the pattern diversity:

$$Dp = 15.3 - 4.6\,(A)$$

Dp = Pattern Diversity Index
A = Area

The distribution of the shape diversity index scores, "Ds," did not approximate a normal distribution. Non-parametric statistical procedures were used to analyze the shape diversity index scores. In a comparison of mesochore and polychore shape diversity index means, there was a significant consensus of association ($p < 0.01$) between the means. The microchore and polychore indentation, protrusion and hole means are listed in Fig. 2. The mode for the shapes approximated a circle. However the median shape was more complex with two protrusions, one indentation and zero holes. Shapes with a diversity index of greater than four, tended to contain holes.

DISCUSSION

From the results, a generalized model can be constructed to guide noospheric prairie form generation within the urban fabric. The model can guide general shape determination of vegetation massings and to guide the orchestration of these shapes into patterns.

Essentially, the shape of vegetation configurations measured in this study appear to indicate that there is a tendency for both species massing shapes and plant community shapes for Minnesota prairies to be similar, regardless of chore classification. The distribution of shapes in a design project could resemble the relative frequency histogram in Fig. 3. Forty-nine percent of the shapes should approximate short fat "C" shapes. Twelve percent of the shapes should approximate long skinny "S" shapes. The remaining percentage should be comprised of complex ameboid shapes. This distribution of shapes is approximately representative of Minnesota prairies. Thus, there are prairie shapes which approximate a circle and shapes which are more complex than a circle. Complex shapes often contain holes and often have nearby circular shapes outside of the main body. The holes are usually simple, with no indentations and no protrusions, meaning the shape of the hole approaches a circle. However, complex shapes are only occasional and not the rule.

The area patterns of vegetation measured in this study appear to indicate that there is a tendency for spatial patterns to decrease in spatial complexity with an increase in chore classification size. The median macrochore pattern edge to area ratio is approximately ten to one. The polychore pattern edge to area ratio is approximately one to one. The macrochore pattern is moderately busy; while the polychore pattern is relatively simple and uniform.

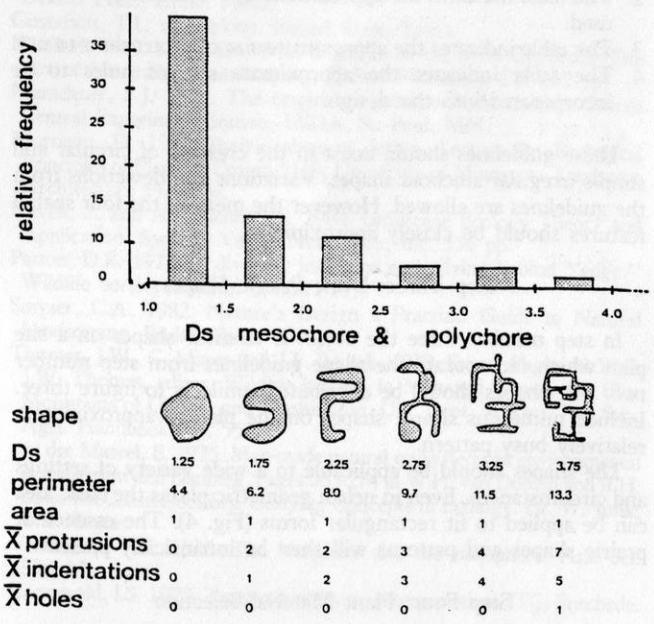

FIG. 3. This figure illustrates the complex distribution and configurations of prairie shapes.

TABLE 2. This table describes the shape guidelines for various size classes of landscapes.

Area	Class	Wavelength	Indentations	Protrusions	Holes	Texture	Ds	DP
<10m^2 PLANTER	Microchore	~1-2m	.5m	1m	0	ultra-fine		
50-1000m^2 YARD	Mesochore	~10-1000m	5-50 m	10-100m	1	fine	simple ~1.25(+2.5)	
5000 to 100000m^2 PARK	Macrochore	1000m	500 m	1000m	10	medium	simple ~1.25(+2.5)	complex ~9(±7.5)
>100000m^2 REGION	Polychore	~>1000m	>500m	>1000m	100	coarse	simple ~1.25(+2.5)	simple ~.5(±.5)

List of Equations:

Equation 1. $DS = \frac{P}{2\sqrt{\pi A}}$ Equation 2. $Dp = \frac{P}{A}$ Equation 3. $Dp = 15.3 - 4.6\,(A)$

Ds= Shape Diversity Index; Dp= Pattern Diversity Index; P= Perimeter; A= Area; π=3.14.

These shape and pattern descriptive measures have applications in landscape design. Providing that one desires to create an urban landscape which visually captures the patterns and shapes of the prairie, one might desire to utilize these descriptive measures. To utilize the model one should utilize the following steps.

Step One: Area Determination

Determine the area destined to become prairie. Examine Table 2 and decide what landscape size class the area best fits. The first class is small planter and dish garden. The second class is the small front or back yard. The third class is about the size of a quarter-section of land or the size of a small park. The fourth class is a region. Determining the class of the landscape is important because it will guide the choice of shapes and patterns.

Step Two: Spatial Guidelines

Utilize the spatial guidelines in Table 2. The guidelines suggest the size of four spatial features to be included in the landscape.

1. The table indicates the wavelength of the curves to be incoporated into the landscape.
2. The table indicates the approximate size of indentations to be used.
3. The table indicates the approximate size of protrusions to use.
4. The table indicates the approximate size of holes to be incorporated into the design.

These guidelines should assist in the creation of circular and simple irregular ameboid shapes. Variations and deviations from the guidelines are allowed. However the mean of the four spatial features should be closely approximated.

Step Three: Draw Prairie Shapes

In step number three the object is to draw shapes on a site plan which incorporate the shape guidelines from step number two. The shapes should be distributed similarly to figure three. Include numerous simple shapes on the plan to approximate a relatively busy pattern.

The shapes should be applicable to a wide variety of settings and circumstances. Even in urban geometric plazas the basic idea can be applied to fit rectangular forms (Fig. 4). The essence of prairie shapes and patterns will then be intrinsically present.

Step Four: Plant Material Selection

Plant material should match the scale requirements of the site. In planters and some small yards, mesic prairie plants may not be appropriate. These mesic prairie plants may be too tall for a small space and can destroy the prairie-like ambience. Instead select the xeric prairie plants and plants with a fine delicate texture; otherwise the prairie landscape design will begin to take on the spatial qualities of a shrubland or young forest stand. If xeric plant material is inappropriate for the site conditions, it may be difficult to capture the visual essence of prairie. Small shrubs may be present at the edges of the meso-landscape. The placement of these shrubs should be similar to the incremental or transitional models described by Diekelmann and Bruner (nd.). Trees may be added to the park and regional landscapes.

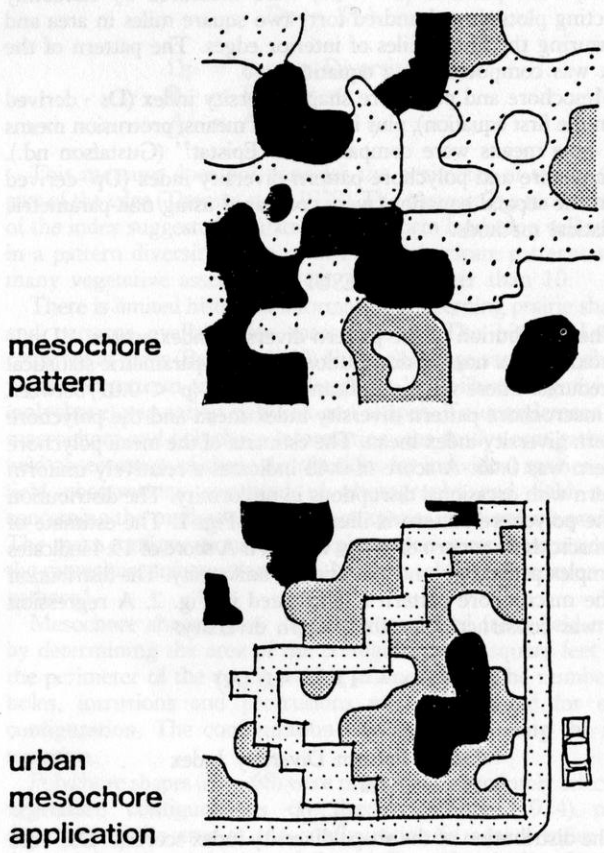

FIG.. 4. Notice how the general prairie shapes and patterns can be applied to even strict geometrical layouts.

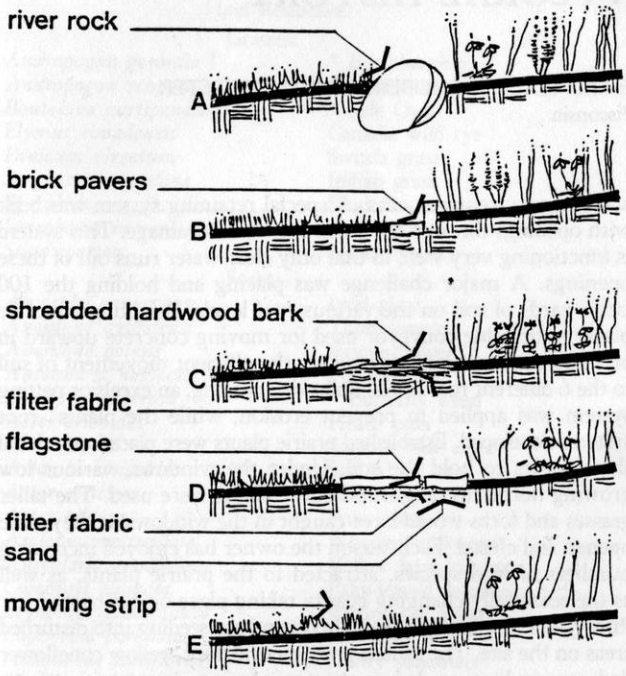

FIG.. 5. This figure illustrates some common methods to define the edge of the prairie.

Step Five: Edge Detail Selection

The physical edge between the prairie and other plant associations is an important component of the design. In planters, edges are controlled by a change in grade and a physical separation. Residential yards are usually too large to be contained by a raised planter. Typically many yards contain or adjoin bluegrass turf. The managed edge between turf and prairie can be critical. Without a discrete edge, maintenance personnel will usually cut into the prairie with their lawn mower. They will slowly reduce the size of the prairie. Figure 5 describes several methods to define the edges of the prairie for a micro-landscape. These methods can be utilized on the most maintenance-sensitive portions of the residential landscape.

The park and regional landscape may not require complex edge details. These landscapes are often defined by roads, fences, creeks, woody vegetation and landform.

This five step process will allow the designer to create landscape shapes and patterns which appear similar to Minnesota prairie shapes and patterns without having to replicate exact prairie landscapes. Some designers might wish to integrate previous design models with this five step process.

CONCLUSION

The native prairie landscapes examined reveal simple shapes forming complex patterns. The quantitative measures described in the design process outlined in this paper can assist the landscape designer to capture the visual spirit of the native prairie for noospheric prairies.

The model generated in this study is essentially a beginning in understanding the shapes and patterns of prairie landscapes. To generate this model, there were some generalizations and statements one may wish to explore further. More samples from the microchore would assist in refining the model. Mesochore information would be helpful in establishing a more accurate regression line to describe pattern diversity from one landscape class to another landscape class. Measurements taken outside Minnesota would be helpful in applying this model to other prairie regions. It would be interesting to apply these measures in the study of woodlands, tundra and tropical vegetation.

There are existing measures to describe shapes and patterns. However, basic research to find more descriptive methods to measure shape and patterns may lead to new insights into prairie form generation. The further development of applied research models could lead to a greater understanding of prairie and incorportaion of prairie landscaping into the urban fabric.

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A ROOF OF WISCONSIN FLORAL HISTORY

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Growing a prairie on the roof of a home is an unique endeavor. The design, material, and aesthetic requirements provided an exceptional landscape challenge. This opportunity arose as an alternate to a "sod roof" on a passive solar home. The owner, Rick Hauf, wanted a sod roof and wanted his home landscape to blend with the adjoining University of Wisconsin-Waukesha prairie restoration. This quote from the "Prairie Seed Source" by Robert Ahrenhoerster briefly explains the uniqueness of prairie:

"[Prairie] can lead you to a very interesting show of rare natural beauty. As your prairie develops and changes from season to season and from year to year you'll have the privilege of witnessing a pageantry of form and color which few people from today's world have ever seen. Your prairie will be a time machine, an opportunity for you to experience and enjoy what the original prairie was like 200 years ago .... Prairie plants have many desirable characteristics. Most are perennial, which means they'll enhance your property year after year without extra cost and effort on your part. As established perennials they'll also tend to crowd out annual weeds, giving you more time for ... doing the other things you enjoy. Prairie plants thrive in full sunlight. They're deep-rooted and drought adapted - no brownout in August! Only seedlings need extra water during droughts. Deep-rooted prairie plants need no fertilizing. In fact your prairie will build up soil fertility naturally, without fertilizer. ... You'll readily appreciate owning these long-lived master of soil and climate, and ... relish the vacation from lawn mowing your prairie will give. ... Restoring Wisconsin prairie will bring you much pleasure and ... you'll enjoy watching your prairie change and develop year after year as it becomes your personal treasury of Wisconsin floral history."

The Hauf residence is a modified earth-sheltered structure with six different roof levels, varying in height from 4 feet to 38 feet above ground level. This earth-sheltered style of architecture lends itself to prairie. The site landscaping consisted of prairie, trees, shrubs and vines, primarily native to Wisconsin. These plants were used to create an informal, low maintenance, landscape around the home. Additional site landscaping included a timber retaining wall constructed to prevent the driveway from washing down into a river running through the property. Spreading junipers and prairie plants were planted outside the passive solar greenhouse/living room. Prickly pear cactus, native to southwestern Wisconsin, was added in this area and thrives, providing a profusion of large yellow flowers each spring. Blending the roof line with the berm on the east side of the home was accomplished as the yellow coneflowers spread from the roof to the site. The wild bergamot, daisies, greyheaded coneflowers and other dry prairie plants provided color on the high slopes. Culver's root, New England asters and palm leaf coreopsis added additional interest on the level garage roof where there usually is an even supply of available moisture. A vegetable garden was moved up on the roof to prevent foraging by wildlife. On the roof prairie grasses and forbs with varying root structures were selected to aid in holding the soil on the roof levels. The plant diversity of over 60 species was possible with the individual habitats provided by the various elevations, slopes, and exposures of the different roof levels. Plant species selection was made to blend with the surrounding oak opening and old field vegetation. The aesthetic benefits of changing colors and textures of the plants throughout the year were also design considerations. The installation of the prairie roof began in fall 1981. A soil type was chosen that provided drainage, and still met the moisture retention requirements to sustain plants growing in one foot of soil. The appropriate loam soil was located within 10 miles of the site and custom mixed with sand to meet stability and drainage requirements. A special retaining system was built with openings through the parapet wall for drainage. This system is functioning very well, in that only clear water runs out of these openings. A major challenge was placing and holding the 100 cubic yards of soil on the various roof levels. Adapting a mobile placer, a drivable conveyor used for moving concrete upward in building construction, allowed for the efficient movement of soil to the 6 different roof levels. Following seeding, an excelsior netting system was applied to prevent erosion, while the plants' root systems developed. Established prairie plants were placed on critical slope angles to hold the soil. Under the windows, various low growing horticultural ground cover plants were used. The taller grasses and forbs would have caught in the windows as they were opened and closed. Each season the owner has enjoyed increasing numbers of bird species, attracted to the prairie plants, as well as the seasonally changing beauty taking place on his roof. After three years, the prairie plants thrive and are seeding into disturbed areas on the site. The switch grass, prairie dock, yellow coneflower and vervain have seeded on the site, serving as a transition from the shrub/mulch areas around the home to the roof-top prairie. The owner has documented energy savings because of the temperature modifying effect of the soil. Snow trapped in the tall grasses and forbs provides additional insulating benefits. In 1985 the Wisconsin Landscape Federation gave an award of merit to this unusual landscape. In spring 1986 a successful controlled burn was done on the lower roof levels. A controlled burn of the upper levels is contemplated for 1987.

FIG. 1. This view, from the southwest, shows 3 of the roof levels. The lowest level is four feet above grade.

PLANT LIST - PRAIRIE AREAS

Hauf Residence

Grasses:

Andropogon gerardia	* Big bluestem
Andropogon scoparius	* Little bluestem
Bouteloua curtipendula	* Side Oats
Elymus canadensis	Canadia wild rye
Panicum virgatum	Switch grass
Sorghastrum nutans	Indian grass
Sporobolus cryptandrus	Sand dropseed
Sporobolus heterolepis	Prairie dropseed
Stipa spartea	Needle grass

Forbs:

Amorpha canescens	Lead plant
Anemone cylindrica	Thimbleweed
Anemone patens	Pasque flower
Antennaria neglecta	Pussytoe
Asclepsia tuberosa	* Butterfly weed
Aster ericoides	Heath aster
Aster laevis	Smooth blue aster
Aster ptarmicoides	Stiff white aster
Aster sericeus	Silky aster
Aster pilosus	Frost aster
Asclepias verticillata	Whorled milkweed
Aureolaria grandiflora	Yellow false foxglove
Coreopsis palmata	Palm-leaved coreopsis
Eryngium yuccifolium	Rattlesnake master
Euphorbia corollata	Flowering spurge
Helianthus laetiflorus	Showy sunflower
Heuchera richardsoni	Alum root
Hieracium longipilum	Longhair hawkweed
Kuhnia eupatoriodes	False boneset
Geum triflorum	* Prairie Smoke
Gentiana quinquefolia	Stiff gentian
Gnaphalium obtusifolium	Sweet everlasting
Lespedeza capitata	Bush clover
Liatris aspera	* Blazing star
Liatris cylindrica	Dwarf blazing star
Liatris ligulistylis	* Blazing star
Lupinus perennis	Lupine
Monarda fistulosa	* Bee balm
Oenothera biennis	* Evening primrose
Parthenium integrifolium	Wild quinine
Penstemon digitalis	Foxglove penstemon
Petalostemum candidum	White prairie clover
Petalostemum purpureum	Purple prairie clover
Phlox pilosa	Prairie phlox
Potentilla arguta	* Tall cinquefoil
Ratibida pinnata	* Grey headed coneflower
Rosa carolina	Meadow rose
Rudbeckia hirta	* Black-eyed Susan
Silphium integrifolium	Rosinweed
Silphium laciniatum	Compass plant
Silphium terebinthinaceum	Prairie dock
Solidago nemoralis	Gray Goldenrod
Solidago rigida	* Stiff (rigid) Goldenrod
Solidago speciosa	* Showy goldenrod
Tradescantia ohioensis	Spiderwort
Verbena stricta	Hoary vervain
Veronicastrum virginicum	Culver's root
Viola pedata	* Birdsfoot violet
Viola odorata	Wood violet

Woodland Edge Plants:
(Indigenous and horticultural cultivars of native species)

Aster novae-angliae	New England aster
Aquilegia canadensis	Wild colombine
Celastrus scandens	American bittersweet
Dodecatheon meadia	Shooting star
Adiantum pedatum	Maidenhair fern
Geranium maculatum	Wild geranium
Monarda didyma "Cambridge Scarlet"	
"Croftway Pink"	Bergamot cultivars
"Snow White"	
Parthenocissus tricuspidata	Boston Ivy
Parthenocissus quinquifolia	Engelman Ivy
Phlox divaricata	Phlox
Physostegia virginiana	Obedient plant
Physostegia virginica vivid	Obedient plant
Polygonatum biflorum	Solomon's Seal
Smilacina racemosa	Solomon's Plume
Tradescantia virginiana	"Pauline" Spiderwort cultivar
Uvularia grandiflora	Merrybells

Cacti:

Opuntia humifusa	Prickly pear cactus

FIG. 2. This west facing entry is covered by prairie on another roof level. The prairie on the tower roof is thirty-eight feet above the "cobble" walk.

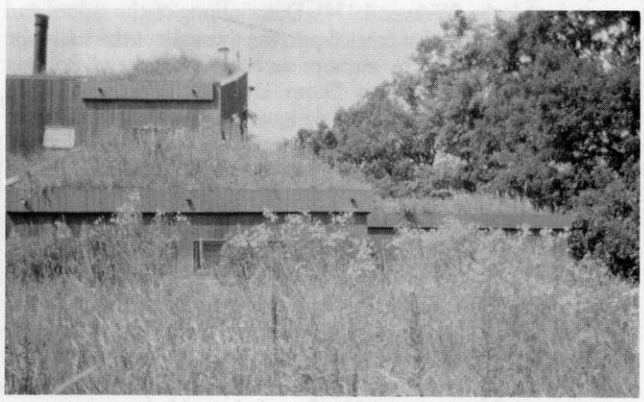

FIG. 3. The grass in the lower part of this photo is on the roof above the entry porch.

FIG. 4. The drainage openings in the parapet walls are visible here. The level prairie on the right is on the garage roof.

INFLUENCES ON FORB SPECIES' VISIBILITY

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Abstract. Five botanical characteristics of plant structure, frequency, blooming frequency, basal cover, density and height, were investigated as to their influence on the visibility of forb species occurring at Avoca Prairie. The area sampled is categorized as wet-mesic. Dominant grasses were *Andropogon gerardi, Schizachyrium scoparium* and *Sorghastrum nutans*.

Three sample areas of 256 contiguous 1/2 m² quadrats each were sampled monthly from June through August. Photographs (35 mm slides) were taken at each sampling area every two weeks from permanent photo stations at distances of 4 and 12 meters.

Through data analysis, basal cover and density were found to be poor measures of a species' visibility. At a viewing distance of 4 meters, height and blooming frequency were the major contributors to a species' visibility. As distance between viewer and sample area increased, the influence of blooming on visibility decreased and that of frequency increased.

Species were assigned a visibility-index indicating their degree of visibility relative to other species, over time and distance. Factors that influenced the visibility of individual species are discussed.

INTRODUCTION

The visual character of the tall grass prairie was first described by many early explorers and settlers as highly picturesque and unique to North America (Shea 1853). These early explorers also described the conspicuous scattered groves of trees within the expansive plain of grass and the patterns that were woven by the grasses and forbs (Weaver 1954). Descriptions of the colors and textures of the plants that created patterns throughout the landscape have since been noted by authors such as Garland and Rolvaag and painters such as Harvey Dunn. During the early 1900's a small number of naturalists and designers also spoke of this visual character when addressing the preservation and reintroduction of prairies into the landscape (Roberts and Rehmann 1929, Jensen 1939, Weaver 1954).

Jens Jensen, for example, attempted to reintroduce the essence of the prairie landscape in many of his midwestern design projects. Two of these are the prairie river at Columbus Park in Chicago and portions of Lincoln Memorial Gardens in Springfield, Illinois. In each instance Jensen placed prairie forbs into unmown lawn and pasture grasses. Jensen's intent was to create a visual resemblance of the prairie community in an attempt to express the regional character and identity of the midwest.

In the past two decades a number of midwestern landscape architects have attempted to simulate or reproduce the aesthetic, and in particular, the visual composition of the prairie community and still maintain a compatibility with natural systems (Morrison 1981). Where Jensen was limited to utilizing species found in the prairie as planting material, many midwest designers today are attempting to combine their design knowledge with prairie ecology to create both visual and structural facsimiles of the prairie community.

Prairie restorations can be categorized as those for scientific studies where duplication of the community structure and functions are the primary objectives and those for aesthetic and/or landscape purposes. This last category, which this paper pertains to, includes designs for industrial parks, public parks, nature centers, roadsides, and residences.

Two sources of information have been relied upon by landscape architects and restorationists when composing a plant community restoration for aesthetic or landscape purposes. Most sources used have concentrated on botanical studies which describe the species of a community and their physical arrangements. However, due to the limited availability of seed sources, costs of forb seed, and present expertise, restorations are generally simplifications of the prairie community (Morrison 1981). One aspect of this is simplification in the selection of the species, their proportions and densities.

The choice of species for the visual portrayal of prairie communities has often been based on botanical indices and lists of high prevalence (Morrison 1980). Thus, the selection of species for visual impact in an aesthetic landscape reconstruction relies on the assumption that those species which have the greatest occurrence or presence based on botanical measures also have the greatest visual presence. This is not necessarily true. For example, *Antennaria neglecta* (pussy toes) may be found with a high degree of frequency and yet has a relatively low degree of visibility. *Lilium michiganense* (western turk's cap lily) is often found at low frequencies but is readily visible.

The second source of restoration information involves the partially subjective judgment made by landscape architects and ecologists, particularly their visual perceptions of a community's composition. Restorations for aesthetic landscape purposes will often increase the proportion of the more visible forbs relative to those of grasses and less showy forbs (Diekelmann et al. 1986). An important aspect of this is the identification of species which are highly visible, i.e., those which can be seen and identified as an entity within a designated distance and at a designated time period. Once these highly visible species are identified, the structural and aesthetic qualities which contribute to their visibility can be determined along with the patterns of color and texture which they collectively create (Stark 1976).

I proposed to investigate the relationships between some of the variables by which species and community structure are commonly studied and the apparent visibility of prairie forb species. The variables of frequency, blooming frequency, basal cover, density, and height were investigated along with time and distance to determine their influence on the visibility of forb species. I also examined the feasibility of creating an index that would be indicative of the relative degree of a species' visibility.

SITE DESCRIPTION

The Avoca River Bottom Prairie, located in northwestern Iowa County, is managed by the Wisconsin Scientific Areas Council and the Bureau of Wildlife Management. The prairie lies on an outwash sand terrace that is patterned with a swell-swale topography and is periodically flooded by the Wisconsin River. The study site is located on one of these swells or ridges. The area is classified as wet-mesic to mesic based on indicator species used by Curtis (1959).

METHODS

A stratified-random sampling method was used to locate three 8 x 8 meter sampling areas. These were each divided into 256 contiguous 1/2 m² quadrats that were sampled at 4 week intervals from June until September for species' presence and for blooming presence. One out of every four of these quadrats was randomly selected for the sampling of basal cover, density, and height for each species present. Height was measured from plant base to its highest vertical point. Basal cover was determined by the percent

area a species occupied at 2 cm - 3 cm above the soil surface. Density was defined as the number of stems a species has emerging from the soil surface within the sampling area. From the data collected on species presence, the average frequency and average blooming frequency for each species found was calculated. Frequency may be defined as the percentage of units in which a species occurs.

Measures, similar to those above, were used to assess the composition of each sample area viewed from set station points. Each 8 meter x 8 meter sample area was quartered into four 4 meter x 4 meter subunits. Permanent photostations as illustrated in Fig. 1 were placed at a distance of 4 meters from the outside edges of each subunit. At this distance the 4 meter x 4 meter subunit filled the viewfinder of a 35 mm camera using a 50 mm lens. A 50 mm lens was selected as a close representation of the cone of vision of the human eye. Photostations were positioned at an eye-level of 5'-5". Color transparencies were taken at two week intervals in an attempt to capture on film all species as they entered and left their blooming stage.

In order to compare the effect of distance on various forb species, photostations were also located at a distance of 12 meters from the sample areas. At this distance the 8 meter x 8 meter sampling areas filled the camera's viewfinder. Although the distance variables throughout this paper are labeled 4 meters and 8 meters, they are actually ranges of 4 to 8 meters and 12 to 16 meters, respectively.

A transparent grid, representing the quadrats used in the previous sampling drawn in perspective to match the viewing distance and angle for each photo taken, was overlaid onto each slide. Using the grid each slide was evaluated for identifiable species in each quadrat. These data were converted to species frequency and species frequency of bloom. A two-dimensional grid was then overlaid on the slides to determine the percent vertical cover a species occupied within the context of the plot. Vertical cover is equivalent to the area of a projected slide occupied by a species and is a function of the species' height and spread.

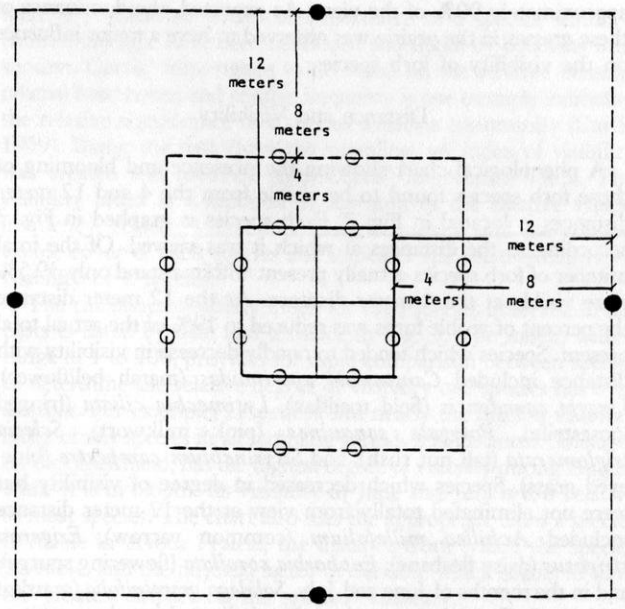

FIG.. 1. Location of photostations.

RESULTS

Nine grasses or sedges were found within the three plots. *Andropogon gerardi* (big bluestem), *Schizachyrium scoparium* (little bluestem), *Carex* spp. (sedge), *Poa* spp. (bluegrass), and *Sorghastrum nutans* (Indian grass) reached an average frequency of 100%. *Andropogon gerardi, Schizachyrium scoparium* and *Sorghastrum nutans* visually dominated each plot occupying

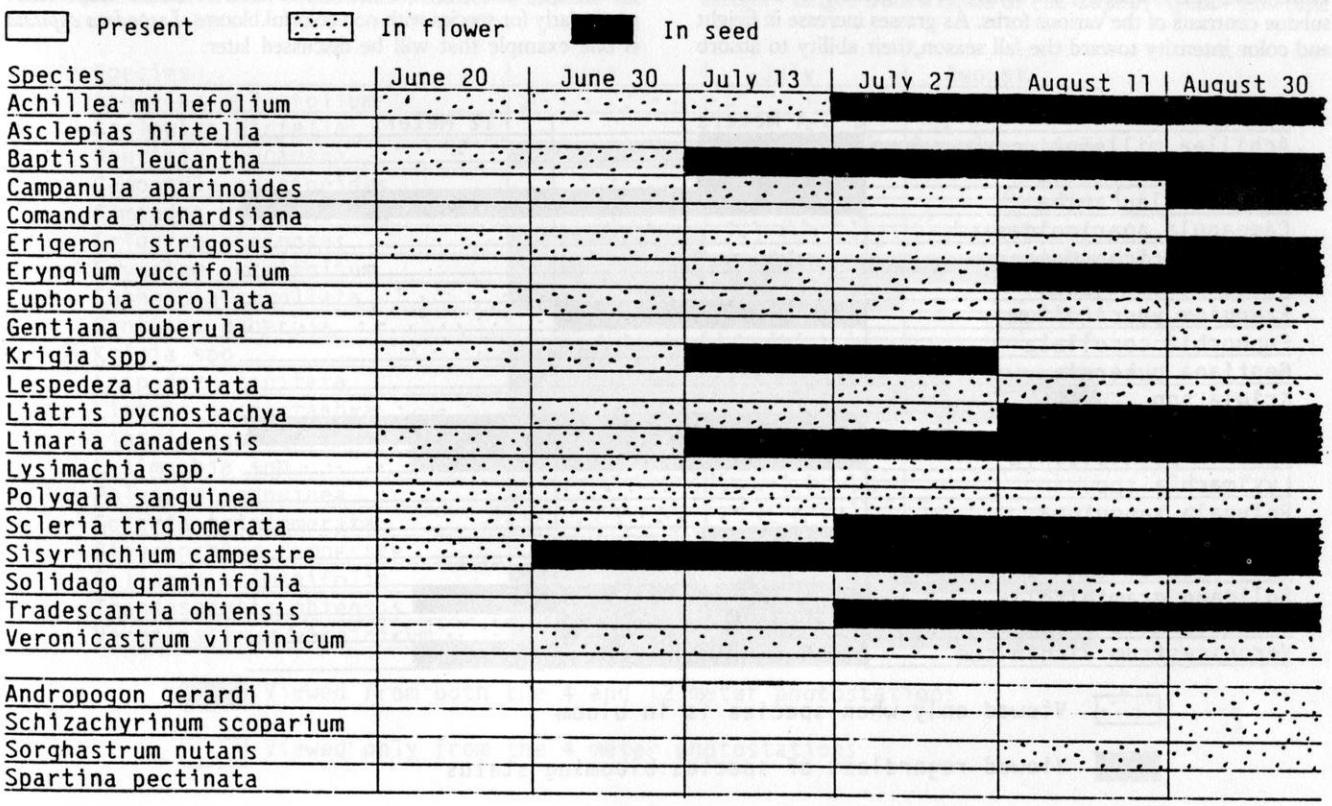

FIG.. 2. Phenological chart.

approximately 90% of the view. As expected, the dominance of these grasses in the prairie was observed to have a major influence on the visibility of forb species.

Distance and Visibility

A phenological chart showing the presence and blooming of those forb species found to be visible from the 4 and 12 meter distances is located in Fig. 2. Each species is graphed in Fig. 3 according to the distances at which it was viewed. Of the total number of forb species actually present within a stand only 39.5% were visible at the 4 meter distance. At the 12 meter distance the percent of visible forbs was reduced to 19% of the actual total present. Species which tended to rapidly decrease in visibility with distance included *Campanula aparinoides* (marsh bellflower), *Linaria canadensis* (field toadflax), *Lysimachia ciliata* (fringed loosestrife), *Polygala sanquinea* (pink milkwort), *Scleria triglomerata* (tall nut rush), and *Sisyrinchium campestre* (blue-eyed grass). Species which decreased in degree of visibility but were not eliminated totally from view at the 12 meter distance included *Achillea millefolium* (common yarrow), *Erigeron strigosus* (daisy fleabane), *Euphorbia corollata* (flowering spurge), and in the months of June and July, *Solidago graminifolia* (grassleaf goldenrod). *Baptisia leucantha* (white indigo), *Lespedeza capitata* (roundheaded bushclover), and *Liatris pycnostachya* (gayfeather) were visible beyond the 12 meter distance.

Time and Visibility

The visible absence or presence of species for June, July, and August is graphed in Fig. 4. Six of the species that were visible all 3 months were *Baptisia, Eryngium yuccifolium* (rattlesnake master), *Lespedeza, Liatris, Solidago* and *Veronicastrum virginicum* (Culver's root). The vegetation context in which a forb exists is important to its visibility. This appears to be largely due to the density and height of the surrounding grasses and their visual absorption capacity, the ability of the grasses to absorb or subdue contrasts of the various forbs. As grasses increase in height and color intensity toward the fall season, their ability to absorb or subdue contrasts in color and form with various species increases. In this study a decrease in the number of visible species occurred between the sampling periods of late July and August.

Influences on the Visibility of Forb Species at 4 Meters

Two sample t-tests were used to determine if significant differences exist between the means of "visible" and "non-visible" species for the measured botanical variables of average height, frequency, blooming frequency, density, and basal cover. Significant differences were assumed for an alpha less than 0.5 and were found to exist for the variables of height and blooming frequency at an observation distance of 4 meters. This indicates, as might be expected, that height and occurrence of bloom are positively related to the potential for a forb to be seen. However, it cannot be assumed that all tall forbs or forbs currently in bloom will have high visibility. Neither should it be assumed that all short forbs or forbs currently not in bloom will have poor visibility.

Data indicate that forb species over 61 cm generally had the greatest potential for being viewed. The densest portion of grasses fell within this height range and may have screened a majority of the lower height species from view. The importance of blooming was evident for a group of 4 species with heights under 20 cm. These species, (*Achillea millefolium, Lysimachia ciliata, Linaria canadensis*, and *Polygala sanquinea*) were visually apparent only when in bloom. Bloom colors that are complimentary to the surrounding green vegetation mass such as pinks and magentas, visually projected through the grasses at a distance up to 6-8 meters. A good example of this is *Polygala*. With a height of 20 cm the pink blooms of this species could be seen through the grasses that towered 60 cm above it. As distance between the plants and viewer increased beyond 4 meters and the density of the grass screen increased, the plants rapidly disappeared from view.

Field observations indicate that while the importance of blooming is partially due to color contrast with surrounding vegetation, contrasting textures and forms are also of major importance particularly for species with non-colorful blooms. *Lespedeza capitata* is one example that will be discussed later.

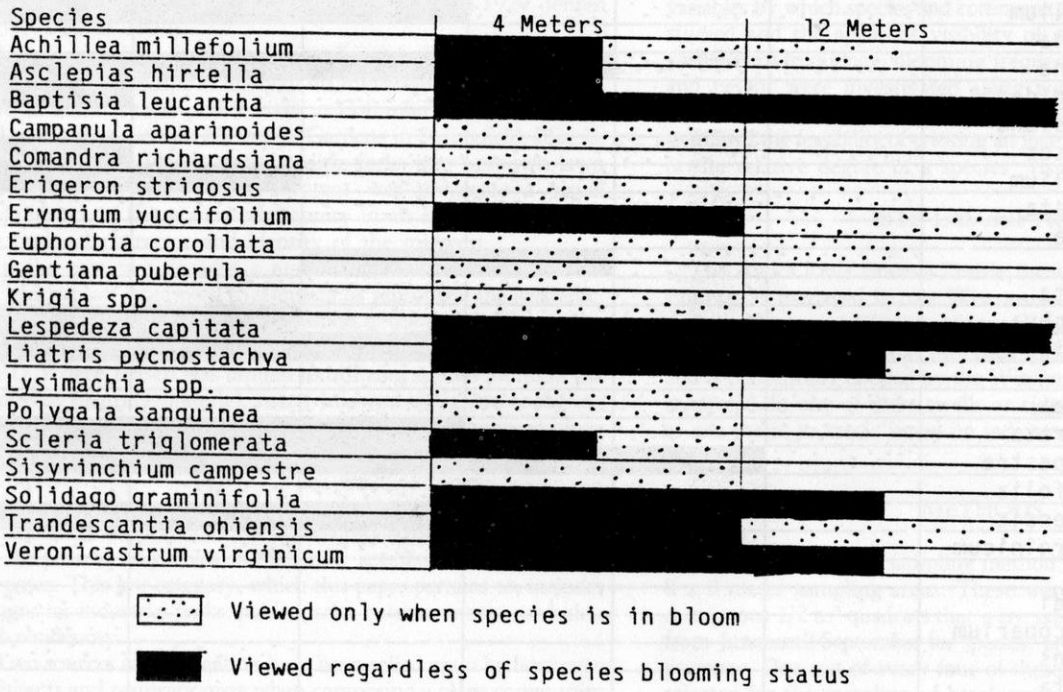

FIG. 3. Forb visibility with distance.

Influence on the Visibility of Forb Species at 12 Meters

At a viewing distance of 12 meters the difference in means for height and frequency between "visible" and "non-visible" species was significant. Blooming frequency was not significant with an alpha value of 0.07. The frequency at which a species occurs appears to have greater influence on its visibility with an increase in distance. At the 4 meter distance blooming appeared to be the characteristic that enhanced the visibility of short species. As distance between the viewer and the individual plant increased, the screening potential of the vegetation mass also increased to a point where short blooming species were no longer visible. As distance increased, blooming could no longer compensate for those species with low frequencies and they disappeared from view.

Dispersion Patterns and Visibility

Dispersion patterns of a random, regular, and aggregated nature were also studied as to their impact on visibility. In general, dispersion pattern does not significantly appear to influence visibility for most species. However, dispersion patterns can play an important role in the character of a prairie or prairie restoration. Observations in the field indicate that single plants of certain species such as *Solidago graminifolia* are difficult to observe at either study distance while groupings are not.

Visibility Index

The selection of forb species for aesthetic/landscape restorations with high visual impact would be aided by the knowledge of a species' degree of visibility at different periods during the growing season and at varying distances. Although we often recognize specific forbs as being extremely showy, the limitations of their ability to be seen over a range of distances or in the context of other species has not been recognized. Perhaps more important is a lack of understanding the design potential of forbs which have more subtle characteristics of showiness. Indices to indicate the relative physical or botanical importance of a species within a community type have been developed and tested by botanists with success. Curtis' importance value based on the relative density, relative basal cover, and relative frequency is one example indicating the relative significance of a species within a community (Curtis 1959). Using the data from the sampling, an index of visibility was created and modeled after Curtis' importance value. The visibility index is a function of the sum of the relative visible frequency, relative visible blooming frequency, and the relative visible cover of each species and indicates the relative degree of visibility of a species.

The calculated visibility index for each species observed in the plots is listed by date and distance in Fig. 5. The index, with a range of 1 to 100, provides for rapid comparison between species to determine the relative degree of visibility one species has over another. For example, *Lespedeza* has nearly the highest visibility index of any species in all sampling periods and distances. *Solidago*, on the other hand, has the highest degree of visibility during August while it is in bloom. Its visibility in June and July is low relative to most species. The chart also lists the appropriate dates a species is visible in Avoca Prairie, the distance from which the species is visible, and the physical factor or variable which seems to have the greatest impact on the species' visibility.

Of the twenty species listed as "visible," eleven had an average frequency of over 50% and six had an average frequency of over 75%. Nineteen of these species were observed flowering during one or more sampling periods. Eight of these were visible only when blooming. Ten of the twenty species had a maximum average height of over 60 cm. Density ranged from less than one plant per 1/2 m² to nineteen plants per 1/2 m².

Twenty-six species found within the study plots were classified as 'non-visible.' Only three of these had an average frequency of over 50% and only one species had a frequency of over 75%. Blooming was restricted to two of these species, *Polygala verticillata* (whorled milkwort) and *Spiranthes cernua* (ladies tresses), both which had heights under 20 cm. Heights for all species in this category ranged from 8 cm to 61 cm. *Oxpolis rigidior* (cowbane)

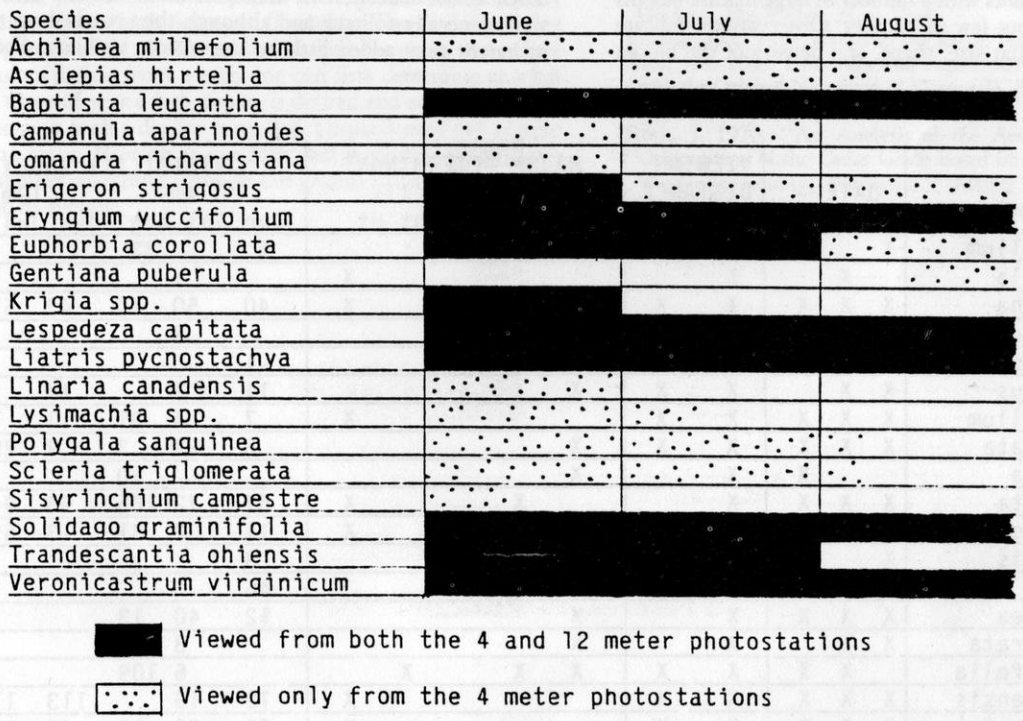

FIG. 4. Forb visibility by month.

was the only species to reach a height of 61 cm. Twenty-one species had densities of less than one individual per 1/2 m². *Antennaria neglecta* had the highest density of all species at 37 plants per 1/2 m².

Individual Species and Visibility

The species with the highest continual visible presence through the summer was *Lespedeza*. Major determinants of its visibility appear to be its height, averaging between 15 cm and 61 cm and its high frequency of 93%. At 4 meters, 92% of the plants found were visible. Although the distinct globular shape of the infloresence and seedhead was apparent from all viewing distances, the flower was visible from neither. The effect of the wind was not tested, however, and may have contributed highly toward this species' visibility in the field. The silver, silky, trifoliate leaves and globular seedhead were conspicuous particularly when the stems waved back and forth in the wind.

Baptisia also had a high visibility index throughout the summer at both 4 and 12 meter distances. This was largely due to its relatively massive canopy structure. The widely branching crown of the mature plant resembles that of a miniature oak tree and is therefore conspicuous in a community that is dominated by the vertical linear element of the grasses. Although the large white flowers were not necessary for the plant to be visible at the distances tested for, they too were highly conspicuous over hundreds of meters. Due to the openness of the foliage, young plants often seemed lost in the grasses. *Baptisia* does not appear to become highly conspicuous until it begins to develop its massive mature canopy.

Veronicastrum had a moderate degree of visibility at both the 4 and 12 meter distances. Its height of 61 cm and mature form of a linear stem with tiers of stiff whorled leaves contributed to its visibility. Blooming did not appear to be a major determinant of visibility. Non-blooming individuals were often visible while many blooming individuals were not. The often loose spire-like white flowers seemed to fade into the surrounding vegetation, particularly, as the incoming light angle increased toward mid-day. Those individual plants with a number of large mature blooms were generally visible but few in number. Observations indicate that along with color that size, shape, and density of the bloom also influence the contribution blooming has toward a plant's visibility. *Veronicastrum* had an average frequency of 93%.

A number of species visually dominated the landscape for only a brief period in the summer. *Tradescantia ohiensis* was visible in June and July primarily due to the blue-violet to almost pink blooms. The slightly pubescent greyish-green leaves added to the species' visibility creating textural and form patterns with the surrounding vegetation. From mid to late July the presence of this plant was observed through the tan seedheads which contrasted against the linear grass growth. As determined through the ratios and noted on the chart in Fig. 5, blooming is the major contributor of visibility for this plant. When in bloom *Tradescantia* added color to the prairie in loosely scattered pockets throughout the area it occupied. After the middle of August, when the foliage died back, *Tradescantia* lost its visibility from both study distances. It had a frequency of 76% and an average density of three plants per square-meter.

A second plant of high visibility in June was *Lysimachia ciliata*. Although the species had an average height of less than 16 cm it was readily seen from the 4 meter distance when in bloom. The individual blossoms are bright yellow and numerous. Foliage is narrow and dull green and did not contribute to the plant's visibility. *Lysimachia* had one of the highest average densities within the study at 25 individuals per square-meter. Only 37% of the individual plants found were visible.

The 10″ candle-like magenta blooms of *Liatris* contributed significantly to its high visibility in July. *Liatris* was also fairly visible in June and August at periods other than blooming. The tall, dark green, grass-like leaves often formed tall dense clusters that excluded the grasses. These were easily distinguished from the grasses due to their darker color and contrasting texture in the 4 meter plots. Blooming plants could be distinguished from the surrounding vegetation at distances greater than 12 meters. At 4 meters 96% of the blooming plants were recorded as visible. At 12 meters 65% were still visible.

Euphorbia was a species with moderate visibility compared to other species tested. Twenty-two percent of the individual plants present were recorded as visible. The white bloom was the species major visible characteristic in mid-summer. The stiff vertical stems were generally solitary and although they reached up to 75 cm in height they added little to the plant's visibility. Short blunt

FORB SPECIES	DATE			VIEWING DISTANCE		MAJOR DETERMINANT OF VISIBILITY					VISIBILITY INDEX 4m			12m		
	Je	Jy	Ag	4m	12m	Blm	Frg	Cvr	Cnt	Ht	Jun	Jul	Aug	Jun	Jul	Aug
Achillea millefolium	X		X	X		X					5	33				
Asclepias hirtella		X		X						X		1				
Baptisia leucantha	X	X	X	X	X					X	40	50	10	43	51	26
Campanula aparinoides		X		X		X						9				
Comandra richardsiana	X			X			X				1					
Erigeron strigosus	X	X		X	X	X					11	2		17		
Eryngium yuccifolium	X	X	X	X	X					X	7	4	31	11	7	11
Euphorbia corollata	X	X	X	X	X	X					6	27	3	7	28	
Gentiana puberula			X	X		X							10			
Lespedeza capitata	X	X	X	X			X			X	57	72	106	93	94	97
Liatris pycnostachya	X	X	X	X	X	X				X	11	32	31	13	65	4
Linaria canadensis	X			X		X					3					
Lysimachia spp.	X			X		X					46					
Polygala sanguinea	X	X	X	X		X					12	40	13			
Scleria triglomerata	X	X		X		X						3				
Solidago graminifolia		X	X	X	X	X	X		X			6	109			160
Tradescantia ohiensis	X	X	X	X	X					X	72	19		113	17	
Veronicastrum virginicum	X	X	X	X	X					X	29	33	11	44	39	

FIG. 5. Forb visibility chart.

leaves that blend well with the grasses contributed to the inconspicuousness of this plant.

Solidago was the visually dominate forb during its blooming period in August. In large colonies, as this forb often occurs, the light yellow-green foliage was conspicuous against the darker background of grasses. When the yellow blossoms opened in August the colonies appeared as drifts of gold moving throughout the prairie. Individual plants were difficult to distinguish and those individuals that were separated from the colony were not readily visible.

The last species to be discussed is *Asclepias hirtella* (green milkweed). The height of this species was over 70 cm, yet this species was relatively inconspicuous. The grass-green linear leaves and light green flower blend very well with the surrounding vegetation . Although tall and stout this species was often difficult to perceive at distances over 1 or 2 meters.

SUMMARY AND DISCUSSION

The understanding and use of data on community structure and environment to determine species which potentially would occur in an area and their relative proportions and distributions is a basic component of any restoration. However, identifying the degree of visibility a forb species may have at various distances and times is a crucial supplemental aid to the designer in the selection of species and their placement.

For example, long distance views that might occur at a highway overlook may desire the use of highly visible forb species compared to close-up views of 1 to 4 meters that could be found in a pedestrian park or a residential lot. In selecting species from those that are adapted to a site, a number or species which are highly visible should be purposely selected. Based on this study, species highly visible at relatively long distances might be *Liatris, Eryngium, Baptisia* or *Dodecatheon meadia* (shooting star) when planted at proper frequencies. *Veronicastrum, Polygala sanquinea* and *Lysimachia* might be planted within a moderate distance from a path while *Gentiana, Sisyrinchium*, and *Asclepias* would often require placement directly adjacent to a path for viewing.

The final placement of a species in a site that is relatively homogenous has a high degree of flexibility. The visibility index may help in that fianl placement. In designing for views that radiate out across a prairie from a path one can first determine at what time or times of year a forb display is desired and at what distance from the path such a display is needed. Displays may not require blooming forbs. *Baptisia* is one forb that is readily visible from long distances marching through the grasses of the prairie when it is not in bloom.

Species placement can be for aesthetic purposes or as an aid for circulation control by placement of forbs as accents and focal points to reinforce the circulation route (Diekelmann et al. 1986). Species which are rare or easily damaged may require the placement of paths beyond the species' visibility range for its protection. Species can also be selected and placed for combination or single displays by their visibility index recognizing time periods at which each species has its highest visibility.

Structural characteristics of height, bloom and foliage texture, bloom and foliage color, and frequency are visibility influences that need consideration in selecting forb species for visually-oriented restoration. Individually these characteristics are not able to predict the degree of visibility a species may have. Variable of specific textures, forms, and color appear to be major factors influencing the visibility of a forb but need further study. Future studies between physical or botanical variables and visual variables have a potential for developing a practical model that would allow the prediction of forb visibility from previously discussed botanical measures.

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A MINNESOTA COUNTERATTACK ON PURPLE LOOSESTRIFE (*LYTHRUM SALICARIA*)

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INTRODUCTION

Alarmed by the possibility that purple loosestrife might be the same perennial which many nurserymen, including myself, distribute, I began an investigation into the taxonomy of the cultivated plants. After a review of the literature and consultations with experts, I maintain that most *Lythrums* sold in Minnesota are one and the same as the invader of our wetlands.

While I shared that information with the Minnesota Nurserymen's Association, I attempted to influence them to discontinue the plants' sale. During this time the Minnesota Department of Natural Resources was sharing information with the public, surveying purple loosestrife's distribution, and suggesting noxious weed status for the plant. Public groups began to also take policy stands.

When funding for the government agency's work was not granted to continue their work, the time was right to pull together my research information and supportive organizations in an attempt to influence public policy. This paper reports the events that have occurred in Minnesota since I first read the Purple Loosestrife Alert (Thompson and Jackson 1980) in 1982 until I organized the Purple Loosestrife Coalition in 1984.

PURPLE LOOSESTRIFE TAXONOMY, IMPACTS, AND CONTROLS

Lythrum virgatum is "much like *L. salicaria*, but glabrous throughout, with the leaves narrowed to the base ... escaped" (Gleason and Cronquist 1963).

Since nurserymen sell both *Lythrum salicaria* and *L. virgatum*, I hoped to prove that at least the latter was safe for me to sell. Although both are distinctive plants in Europe, United States taxonomists (Gleason and Cronquist 1963, Fassett 1975, Swink 1979, Magee 1981) did not concur on their descriptions of plants found in the Midwest. *L. virgatum* was not mentioned by all and I feared misidentification was possible.

In the summer of 1983, Dr. Thomas Morley of the University of Minnesota Botany Department visited Twin Cities nurseries and observed *Lythrum salicaria* sold as different cultivars, none of them actually *L. virgatum*. He also noted that no collections of *L. virgatum* found in Minnesota appear in the University of Minnesota Herbarium (Morley, personal communication). These observations suggest that either none of the *L. virgatum* has escaped to the wild or the plants are erroneously identified in the Minnesota nursery industry. Taxonomic research is needed to resolve this question.

"Most of the garden *Lythrums* are of hybrid origin and are certainly desirable plants" (Snyder 1983).

To complicate the identity problem, records do not agree on the parentage of most garden hybrids (Buckley 1977, Giles 1980, Still 1982, Snyder 1983). Hybrids like "Morden Gleam," "Dropmore Purple" and "Morden Rose" are claimed by both parents which is thought to be genetically impossible. Morden Arboretum suggests using its introduction "Morden Pink," which is believed to be seedless. Morden researchers add that only further study will show if it could produce seed if certain incompatibilities are satisfied (Collicutt, personal communication). This suggests that research is necessary if doubt about the hybrid's escape potential is to end. Concern remains since hybrids are thought capable of reverting in 3-4 generations (Pellet, personal communication). Let us not forget that the plant not only reproduces by seed but also vegetatively (Thompson and Stuckey 1980).

"The spread of loosestrife has been aided in part, by its aesthetic appeal" (Pfannmuller and Djupstrum 1983).

Much of nurserymen's sales stem from that aesthetic appeal in gardens. If studies could monitor the garden site, we could learn if the plant moves easily and consequently jeopardizes wetland quality. Typically loosestrife is planted in gardens with high and dry environments. Although the plant is able to tolerate a wide range of moisture and soil conditions, such a site might be found to stress the plant and cause it to merely survive in place, rather than flourish and spread. Then the use of the plant would seem safe.

Nevertheless, nurserymen do not limit their sales to high and dry gardens. Seeds and seedlings are also sold for wetland use for value as wildlife food and cover, bees' nectar sources and enhancement of man-made ponds. Value of the plant for wildlife food and cover has proven minimal and even disastrous when *L. salicaria* displaces native plants (Rawinski 1981). Although used as a pollen source in the East, beekeepers give conflicting reports on quality and yield of honey derived from purple loosestrife (Pellet 1976). The U.S. Department of Agriculture does not list the plant among suggested nectar and pollen plants (U.S. Department of Agriculture 1980). Purple loosestrife's aesthetic value in a wetland would seem difficult to dispute. However, once wetland owners are aware of the lowered wetland quality that results, they do not perceive the plants to be beautiful (Skophammer 1982).

Purple loosestrife infestation is defined as "plants established in each square mile of wetlands drainage" (Thompson and Stuckey 1980).

When these seeds or seedlings are planted directly into a wetland, an infestation follows. Primary Midwestern distribution of purple loosestrife is within the boundaries of the Wisconsin Glaciation, which includes all of Minnesota (Stuckey 1980). Whether the plants have been purposefully seeded or have naturally migrated from the East coast, nearly one half of Minnesota's counties are already infested (Djupstrum, personal communication). During the blooming period between July 1 and September 10, the extent of the problem is visible throughout southeast Minnesota. Some 20,000 acres of Minnesota's wetlands were affected by 1978 (Thompson and Stuckey 1980).

The impacts on Minnesota's wetlands, a prime part of the prairie pothole waterfowl production area include: (1) outcompeting native plants, (2) threatening wild rice production, (3) lowering species diversity, (4) reducing food and cover for muskrats, marsh wrens, black terns, Canada geese, mallards, shorebirds and bog turtles, (5) degrading wetland hayfield and pastures and (6) lowering resale value of wetlands (Rawinski 1981, Stuckey 1980, Thompson and Stuckey 1980).

"In a dramatic botanical takeover, a runaway species from abroad - a purple tide - has displaced indigenous plants" (Teale 1983).

Although deliberate planting hastens purple loosestrife's spread, records show that the plant had already escaped in the eastern United States in the 1800's. Its apparently slow rate of spread is deceiving. Sometimes it establishes and does not explode into great numbers until as much as 50 years later (Thompson and Stuckey 1980).

However, where wetlands are disturbed by construction or water manipulation, rapid outbursts are documented. In New York, a 12 acre man-made pond became dominated in three years (Thompson and Stuckey 1980). Also in New York where water manipulation was used as a management tool in the Montezuma National Wildlife Refuge, it expanded from 10 to 1,000 acreas in twenty years time (Rawinski 1981). In Horicon National Refuge in Wisconsin, some 25 acres of the 16,000 parcel were dotted with the plant in 1981. After a drawdown, some 400 acres were infested within three summers (Dottie Thompson, personal communication).

The before-mentioned impacts and rate of spread have prompted experimentation with such management methods as: (1) burning, which has little success, (2) mowing and grazing, which are little documented, (3) plowing and disking, which work on accessible topography, (4) water manipulation, which favors population expansions, (5) species replacement, which often means substituting one exotic for another, (6) biological controls, which will take many years of research, (7) hand pulling, which is labor intensive and (8) herbicide control, which is costly and not proven environmentally safe (Evans 1982).

At this time, biological controls are thought by many to be the most ecologically sound control. To buy time for research, some managers are attempting to contain purple loosestrife with chemicals, especially glyphosate. Glyphosate is marketed by Monsanto under the brand name "Rodeo" for water use, and is apparently 99% effective. Cooperative experiments have been set up with Monsanto and some of the U.S. Fish and Wildlife Service refuges to determine an effective rate and time that could limit this nonspecific herbicide on sites including refuges at Minnesota Valley and Sherburne in Minnesota and Horicon in Wisconsin (Larson, personal communication).

SHARING THE INFORMATION WITH THE NURSERYMEN

(Regarding *Lythrum*) ... "the facts as best we know them so we can determine what needs to be done and what we as responsible nursery people should be recommending" (Selinger 1984).

Because I believe a ninth control - not selling *Lythrum* - should be added to the list of controls, I suggested to many gatherings of nurserymen that they voluntarily stop its sale. After all, a precendent had been set some 25 years ago when common buckthorn (*Rhamnus catharticus*) was eliminated from nursery catalogues in Minnesota. The plant had proven to be a host for a fungus that harmed grain crops. I appealed to their land ethic with the life history, impact, and control information described earlier. If those facts did not influence their opinion, the fact that their tax money is paying for control efforts by the U.S. Fish and Wildlife Services and Department of Natural Resources in Minnesota was offered. Finally, I pointed out that this perennial accounts for an insignificant portion of annual sales and not selling it would have minimal impact on their profits (U.S. Department of Agriculture 1984).

The minimal economic value did not offset the potentially negative public relations value and many nurserymen agreed to cease its sale. After hearing my findings, the Minnesota Nurserymen's Association Plant Materials Committee with an endorsement from the Executive Board of Directors issued the following warning to its membership (Selinger 1984). The warning was a compromise and condemned only *Lythrum salicaria* and some of its cultivars. However their statement signifies a new level of awareness and cooperation:

Dear Minnesota Nurserymen:

The MNA Plant Materials Committee has been studying the problem of *Lythrum salicaria* (Purple Loosestrife) during recent months. This aggressive perennial has been displacing other aquatic and riparian plant species in the wet areas of Minnesota over the past few years, reducing waterfowl habitat and ecological diversity. The problem is that we, as nurserymen, may be selling *Lythrum* varieties which contribute to the problem, namely those which become aggressive in the wild and/or produce viable seed.

After requesting guidance from the Minnesota Department of Natural Resources, we received a letter from the DNR which requested that sale of purple loosestrife in the state be stopped within two years. The MNA Board of Directors is therefore recommending to the membership that their *Lythrum* growing and marketing plans be reviewed and modified to remove varieties which have aggressive tendencies, set viable seed, or have *L. salicaria* as a parent. Information on parentage is limited and, in some cases, conflicting, but the following varieties appear to be acceptable in terms of parentage and seed set: Dropmore Pink, Morden Pink, Rose Queen, and The Rocket. This list is not intended as the last word on the subject, but rather as a beginning toward an industry effort to police itself.

The DNR is very serious in its quest for removal of purple loosestrife from the area. They have even considered an attempt to have the plant listed as a noxious weed. We, as an association, have an obligation to be leaders when problems arise. The danger to our wetlands has been clearly demonstrated, and a positive response to the problem will clearly reflect our concern.

ACTION BEYOND THE NURSERY INDUSTRY

"First, do not purchase the plant for use either as an ornamental or as a source of nectar; second, remove any stand that you may have started in a ditch or flower garden and inform your neighbors of the threat this invader poses before they plant it; third, when you see purple loosestrife blooming in a wetland in midsummer, notify the U.S. Fish and Wildlife Service ..." (Pfannmuller and Djupstrum 1983).

In addition to the "Purple Loosestrife Alert" written by the U.S. Fish and Wildlife Service in 1980 that motivated my research, other articles were being written by government agencies to increase public awareness. The above information was part of an education effort by the Minnesota Department of Natural Resources in 1983. After they conducted a survey of their wildlife managers to learn the extent of loosestrife distribution, they decided a need for research and containment existed. In a special effort to find funds for these purposes, they attempted to add the plant to the noxious weed listing. When opponents called for a hearing, the department realized that neither staff or money were available to pursue the listing. Also a proposal for funding the control of the plant was submitted to the LCMR without success ending in May of 1984.

In the meantime increased awareness in the public sector prompted the following action in Minnesota: (1) the Izaak Walton League resolved to "encourage the inclusion of purple loosestrife on the list of noxious weeds ... and propose (d) the prohibition on intrastate commerce of the plant," (2) the Audubon Chapter of Minneapolis resolved "the inclusion of *Lythrum salicaria* on the list of noxious weeds" and urged Minnesota agencies to investigate the problem and seek a solution to eradicate the species, and (3) the City of Chanhassen added wetland protection regulations to the City's Zoning Ordinance No. 47. By doing so "the planting any species of the genus *Lythrum* is prohibited in Class A or B wetlands (types 2, 3, 4, 5, 6, 7 and 8 per the U.S. Fish and

Wildlife Services Circular 39)'' (personal communication with each organization). These actions occurred during the summer of 1984.

A POST CONFERENCE UPDATE - Because Minnesota nurserymen had stated a desire to cooperate, because the Department of Natural Resources had acted but needed further funding, and because public organizations had begun to take a stand on the issue of purple loosestrife, the time was optimum to coalesce support. I formed the Purple Loosestrife Coalition on November 12, 1984. Thus what began as my search for information evolved into a move towards legislation. Legislation that would lead to funding was the prime goal of the Coalition. The group included: Friends of the Minnesota Valley, Audubon Minneapolis Chapter, Izaak Walton League, HATPIN, Minnesota Waterfowl Association, Sierra Club, Minnesota Wildlife Society, Chanhassen Environmentalists, and Minnesota Conservation Federation. Support came from other individuals, agencies and organizations who could not be politically active. The group included members with scientific knowledge, political savvy, environmental clout, nursery industry insight, wildlife habitat understanding and natural resource experience. In April of 1985 Representative Connie Levi proposed the legislation below drafted by the Purple Loosestrife Coalition to control the sale of purple loosestrife.

A bill for an act

relating to purple loosestrife (*Lythrum Salicaria*) and its cultivars; prohibiting the propagation, sale, or introduction of the plant into Minnesota; amending Minnesota Statutes 1982, Section 18.335.

BE IT ENACTED BY THE LEGISLATURE OF THE STATE OF MINNESOTA:

Section 1. Minnesota Statutes 1982, Section 18.335, is renumbered and amended to read:

18.3356 [PENALTY]

Any person violating any of the provisions of Sections 18.331 to 18.3345 is guilty of a misdemeanor.

Section 2. Minnesota Statutes 1982, Section 18.335, is replaced to read:

18.335 [SALE OF PURPLE LOOSESTRIFE FORBIDDEN]

Purple loosestrife (*Lythrum Salicaria*) and its cultivars are non-native plants that seriously disrupt pastures, meadows, native wildlife plant habitats, and wetlands. The propagation, sale or introduction of purple loosestrife (*Lythrum Salicaria*) and its cultivars into the state is forbidden.

Section 3. [EFFECTIVE DATE]

This Act is effective Sixty (60) days after its final enactment.

The Minnesota Department of Agriculture requested and was granted review of the proposed legislation so that they could determine whether it could be addressed under existing legislation. After the review they proposed that (1) the plant be listed as a noxious weed seed, (2) the nurserymen continue their voluntary ban, and (3) further effort be made to educate the public. The Department also proposed that they and the Department of Natural Resources jointly sponsor legislation to fund the control of purple loosestrife. Since their action in June of 1985, an interagency work group has been formed that includes: the Department of Natural Resources, the Department of Agriculture, the Minnesota Department of Transportation and the U.S. Fish and Wildlife Service. This agency coalition knows it has public support from this point on.

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