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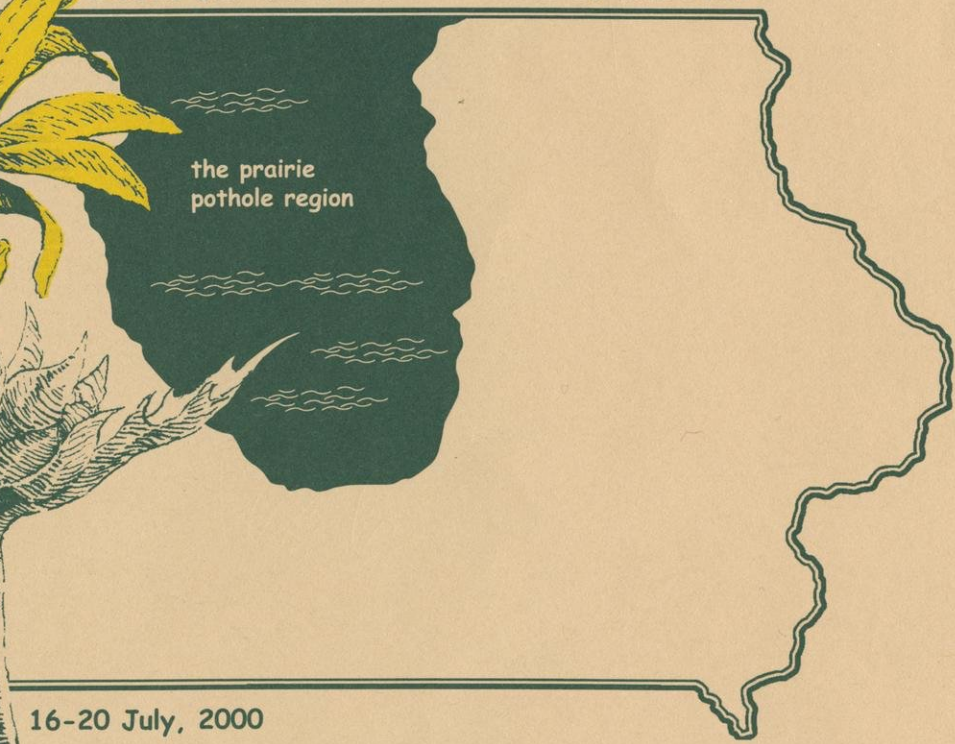
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Proceedings of the 17th North American Prairie Conference

Seeds for the Future ~ Roots of the Past



16-20 July, 2000
North Iowa Area Community College
Mason City, Iowa

PAST NORTH AMERICAN PRAIRIE CONFERENCES

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- 1st
14-15 September
1968
Illinois
Schramm, Peter, Editor. 1970. Proceedings of a Symposium on Prairie and Prairie Restoration. Knox College Biological Field Station Special Publication No. 3. Knox College, Galesburg. 66 pages. [For copies, make checks for \$5.50 (U.S.) postpaid payable to Peter Schramm, Knox College, Galesburg, IL 61401.]
- 2nd
18-20 September
1970
Wisconsin
Zimmerman, James H., Editor. 1972. Proceedings of the Second Midwest Prairie Conference. Madison, Wisconsin. Published by the editor. 242 pages. [For copies, make checks for \$8.50 (U.S.) postpaid payable to: James H. Zimmerman, 2114 Van Hise Ave, Madison, WI 53705.]
- 3rd
22-23 September
1972
Kansas
Hulbert, Lloyd C. (c/o David Hartnett), Editor. 1973. Third Midwest Prairie Conference Proceedings. Division of Biology, Kansas State University, Manhattan. 91 pages. [For copies, make checks for \$6.00 (U.S.) postpaid payable to: Konza Prairie Office - Division of Biology, Kansas State University, Manhattan, KS 66506.]
- 4th
19-22 August
1974
North Dakota
Wali, Mohan K., Editor. 1975. Prairie: A Multiple View. The University of North Dakota Press, Grand Forks. 433 pages. 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. University of North Dakota Press, Grand Forks. 466 pages. [Neither publication is available for purchase.]
- 5th
22-24 August
1976
Iowa
Glenn-Lewin, David C. and Roger Q. Landers Jr., Editors. 1978. Proceedings of the Fifth Midwest Prairie Conference. Extension Courses and Conferences, Iowa State University, Ames. 230 pages. [For copies, make checks for \$3.50 (U.S.) postpaid payable to: Botany Department Education Fund. Send to Joanne Nystrom, Department of Botany, Iowa State University, 353 Bessey Hall, Ames, IA 50011.]
- 6th
12-17 August
1978
Ohio
Stuckey, Ronald L., and Karen J. Reese, Editors. 1981. The Prairie Peninsula, In the Shadow of Transeau: Proceedings of the Sixth North American Prairie Conference. Ohio Biological Survey Biological Notes No. 15. 278 pages. [For copies, make checks for \$18.00 (U.S.) postpaid payable to: Ohio Biological Survey, 1315 Kinnear Rd., Columbus, OH 43212-1192.]
- 7th
4-6 August
1980
Missouri
Kucera, Clair L., Editor. 1983. Proceedings of the Seventh North American Prairie Conference. Southwest Missouri State University, Springfield. 321 pages. [For copies, make checks for \$10.00 (U.S.) postpaid payable to: Southwest Missouri State University. Send to Wallace R. Weber, Department of Biology, Southwest Missouri State University, Springfield, MO 65804.]
- 8th
1-4 August
1982
Michigan
Brewer, Richard, Editor. 1983. Proceedings of the Eighth North American Prairie Conference. Department of Biology, Western Michigan University, Kalamazoo. 176 pages. [For copies, make checks for \$22.00 (U.S.) postpaid payable to: SWMLC. Send to Southwest Michigan Land Conservancy, 6851 South Sprinkle Road, Portage, MI 49002.]
- 9th
29 July-
1 August
1984
North Dakota
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 Centre for Environmental Studies, Moorhead. 264 pages. [For copies, contact Richard H. Pemble; make checks for \$20.00 (U.S.) postpaid payable to: Tri-College University, 306 Ceres Hall, North Dakota State University, Fargo, ND 58105.]

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North Iowa Area Community College
Mason City, Iowa

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Seeds for the Future ~ Roots of the Past

The prairie heritage celebrated at North American Prairie Conferences (NAPCs) began thousands of years ago. Part of the vast historic prairie ecosystem, the tallgrass prairie, built the soils of the American Midwest that today sustain much of the world's population with food crops. Surely the seeds for the future were nourished by the roots of the past. Unfortunately, the giver of all that nourishment, the prairie itself, has almost entirely been lost in the process. Scattered patches of grasslands and rare potholes around the continent give us both a breathtaking glimpse of the ecosystem responsible for our abundant crops, as well as a sad reminder of the cost of developing our agricultural system.

Thankfully, our prairie heritage includes much more than the soils and the plants. The people of the prairie were and are very special. It is heartwarming, inspiring, and affirming to be among people who honor and preserve the magnificent beauty of the prairie. Certainly my association with "persons of the prairie" was central in my decision to accept the challenging opportunity to chair the 17th NACP. Helping facilitate a gathering of prairie people from all over the continent is a special privilege. Prairie people are *of* the earth, often carrying some under fingernails; they are *by* the earth, sweltering in relentless heat to cut cedars, harvest seed, survey insects; and surely they are *for* the earth in all its native glory. What more honorable group of people could be assembled?

This must be part of the reason that the idea of a large prairie conference gathering was initiated in 1968, officially becoming the North American Prairie Conference in 1978. At these meetings, people from all walks of life, from amateur photographers to zoologists, come together every two years to celebrate the beauty that is, was, and forever shall be, the prairie. In the words of John Sawhill, we believe that "*in the end our society will be defined not only by what we create but by what we refuse to destroy.*" Not only do we refuse to destroy the prairie, we work diligently to educate and inspire others to appreciate and protect remnants of the ecosystem that once covered so much of the central continent. While others marvel at skyscrapers and automobiles, we are awestruck by grassland fires and tiny butterflies.

So it was that six hundred and seventy people gathered at the 17th North American Prairie Conference at North Iowa Area Community College (NIACC) in Mason City, Iowa, 16–20 July, 2000 to share knowledge, story, art, and, ultimately, their love of the prairie. Twenty-six states and three Canadian provinces were represented. It was interesting, in our opening session, to recognize those persons who had attended a number of the past sixteen North American Prairie Conferences. Several had been to each event; they are the roots of our association. It was perhaps more gratifying, however, to identify a large number of persons for whom this was their first ever prairie conference. They must have numbered over one hundred. Hopefully, seeds were planted and nurtured in those participants to carry on the great tradition of gathering to celebrate prairie!

The 17th NACP began with Tom Rosburg of Drake University summarizing Iowa's prairie heritage and taking a look toward the future. Deb Lewis of Iowa State University gave us a glimpse of some of Iowa's early prairie preserve personalities, and Dick Leet of

the MacNider Museum in Mason City shared his concepts and art of Midwest landforms. Attendees enjoyed ninety concurrent sessions and poster papers presenting information on restoration and management, education and heritage, animals and animal ecology, and plants and plant ecology. Two symposia were organized by staff of the Native Roadside Vegetation Center at the University of Northern Iowa. The Roadside Management Symposium was hosted by Kirk Henderson, Iowa Integrated Roadside Vegetation Management program manager. A "Seed Source Issues in Prairie Reconstruction" symposium was moderated by Greg Houseal, manager of the Iowa Ecotype Project. The efforts of these individuals, and their invited speakers, added a great deal to the conference and are much appreciated.

Iowa environmental educators, Carole Kern and Mary Norton, and Kathy McKee, Mike Blair, and Randi Montag-Peterson conducted education workshops. Brian "Fox" Ellis of Peoria, Illinois and Sara Griffin-Hoofnagle of the National Wildlife Federation in Colorado provided additional workshops for teachers. These sessions were attended by an unexpected broad range of participants, and I regret that there were seating problems at times. Bill Koch of the University of Northern Iowa entertained us with Walt Whitman's life and thoughts after the Tuesday barbeque, and Frank Oberle of Kirksville, Missouri shared his beautiful slides after the Wednesday night banquet. The Tuesday field trips were a highlight, with participants traveling up to one hundred twenty-five miles to enjoy some of Iowa's native and restored prairies. It was a week full of discussions, large and small, centered on the importance of sustaining and enjoying prairie.

I gratefully acknowledge the services of the primary planning committee members. Daryl Smith mentored me every step of the way, for fifteen months. Neil Bernstein and Tom Rosburg kindly reviewed abstracts and helped plan the concurrent sessions. Paul Christiansen put together a phenomenal array of field trips. Craig Zoellner not only facilitated the vendor services and the field trip transportation, but also listened and counseled (and consoled) during the months of preparations. Each of these gentlemen were unwavering in their support, and each faithfully and punctually responded to my numerous queries and requests.

Certainly we are all indebted to the contributors of the conference. The Iowa Department of Transportation gave significant support for publication of these proceedings through a grant from the Iowa Living Roadway Trust Fund. An Iowa Resource Enhancement and Protection (REAP) grant funded attendance by twenty-five Iowa teachers. Other financial and in-kind contributors included: American Cyanamid, Alliant Energy, Land and Water Magazine, Ruth May, The Minnesota Native Wildflowers/Grass Producers Association, the NIACC Foundation, PrairieSource.com, Salix Ecological Resources, Peace Coffee, The Truax Company, Inc., Eric Howes-Vonstein, Ernst Conservation Seeds, Cedar River Garden Center, CRM Ecosystems, and the University of Iowa Press.

I dare not begin to attempt to individually acknowledge the other numerous volunteers and NIACC staff who so cheerfully lent their expertise, opinions, and labor to this event. There are well over one hundred people who contributed to making this conference memo-

able. I am infinitely grateful for the willing and kind support of the session moderators, concurrent presenters, field trip leaders, banquet servers, registration material organizers, symposium presenters, vendors, registration staff, custodial staff, entertainers, and, of course, the attendees! The conference was truly a highlight of my life.

Neil Bernstein and Laura Ostrander (a former NIACC student) have done an incredible job of editing these proceedings. Neil's expertise and efficiency has been thoroughly amazing; I feel very fortunate that he accepted the task of editor. And we found an outstanding and enthusiastic assistant in Laura, a senior majoring in English at Luther College in Decorah, Iowa. We feel she is well on her way to a very successful career in editing and writing.

I thank all people across this continent that have helped establish

a firm foundation of respect for prairie, and I congratulate all who continue to work to ensure that the seeds for the prairie's future find fertile and hospitable ground. I look forward to seeing you at Kirksville!

Carol W. Schutte

Editors' Note: As editors always get the final word, we want to thank all the reviewers who read the manuscripts as well as the authors who responded to our numerous requests for revisions. We also thank Carol for all the long hours, hard work, and dedication that made this conference and proceedings a success.



Iowa's Prairie Heritage: From the Past, Through the Present, and Into the Future

Plenary Address

THOMAS R. ROSBURG

Department of Biology, Drake University, Des Moines, Iowa 50311

Welcome to Iowa, the heart of the tallgrass prairie, and to the 17th North American Prairie Conference. One of the remarkable aspects about this conference is that over the last 34 years it has evolved into a unique gathering of prairie-addicts—from farmers, nursery managers, and landowners to landscape architects, naturalists, and scientists. A diversity of humans that mirrors the biological diversity of prairie, all gathered for a common purpose—to celebrate our understanding and knowledge, the importance and value, and the sheer beauty of one of the largest biomes on the continent. In doing so, this conference provides a wonderful opportunity to travel to all corners of the prairie biome to observe and learn about the multitude of variations in its communities, organisms, and culture.

Since the conference was last held in Iowa in 1990, conference participants have explored mesic tallgrass prairie and savanna at the Ojibway prairie near Windsor, Ontario; dry tallgrass at Konza Prairie in Kansas; black oak savanna at Nachusa Grasslands in northern Illinois; and most recently, mid-grass and mixed prairie in the deeply dissected loess landscapes of central Nebraska.

Now, here we are back in Iowa for the third time since it all began at Knox College in 1968. All signs indicate it will be a great conference. Carol has really put together a great schedule of speakers, activities, and fieldtrips. My job this morning is to help kick it off with an overview of Iowa's prairie heritage. Simply put, I'll try to take you on a tour of Iowa to see the "past, present, and future" condition of prairie in Iowa.

Before I start, I would like to take a moment to dedicate this presentation to the memory of Kyle Swanson, who was tragically killed in a highway accident last March. Kyle was a dear friend and colleague to many of us attending the conference and a devoted enthusiast of prairie conservation and education in Iowa. He is greatly missed; although I have no doubt that his spirit will truly be with us this week.

My plan for this morning's slide show is to start with the past and work towards the future. I'll try to give you a sense of the presettlement prairie landscape in Iowa, especially its diversity, which I suspect was as great or greater than in any other prairie state. We'll also focus on the environmental factors that were important in its development and maintenance. Then we'll take a look at existing prairie remnants around the state, some of which many of you will see on your field trips. And we'll finish with some thoughts about the future of prairie in Iowa—what can we look forward to and perhaps what challenges and problems may lie ahead.

A LOOK AT THE PAST

On most of my excursions throughout the state I seem to be drawn to a familiar question—what did this landscape look like prior to

settlement? My eyes scan the countryside for clues—the extant vegetation and its structure, the geomorphology, the pattern of agriculture. One of the best ways to answer that question is to look at the historical data. Foremost are the Government Land Office (GLO) surveys conducted in Iowa between 1832 and 1859. Notes of the surveyors have been digitized for the entire state and can provide a picture of the native landscape (Fig. 1). These data indicate that prairie communities occupied about 85% (30 million acres or 12 million ha) of the state. A very clear pattern can be seen—greater extensiveness of prairie towards the west and greater mosaic of prairie, savanna, woodland, and forest in the east.

Another important source of historical data is the many written accounts and diaries of early explorers and settlers. The first example comes from John Madsen's celebration of the prairie—*Where the Sky Began* (Madsen 1982). This is a general description taken from a gazette of the time (ca. 1860):

The attraction of the prairie consists of its extent, its carpet of verdure and flowers, its undulating surface, its groves, and the fringe of timber by which it is surrounded. Of all these, the latter is the most expressive feature—it is that which gives character to the landscape, which imparts the shape, and marks the boundary of the plain. If the prairie be small, its greatest beauty consists in the vicinity of the surrounding margin of woodland, which resembles the shore of a lake indented with deep vistas, like bays and inlets, and throwing out long points, like capes and headlands.

The next two examples are observations made during military explorations of the Iowa Territory. The first includes excerpts from the diary of an anonymous soldier on the expedition of Kearny and Lea (Anonymous 1835). Their route followed the Des Moines River from the southeast corner up through central Iowa to about Fort Dodge, and then proceeded overland through north-central Iowa to the Minnesota border:

Marched 16 miles over a marshy prairie . . . The prairies on this section are covered with strawberries . . . marched 25 miles over dry prairie . . . Our Indians kill much game mostly deer . . . marched 20 miles over an almost boundless prairie . . . This evening killed an elk . . . Encamped on the Cedar River. Killed several buffalo . . . Encamped in the open prairie without wood and bad water and consequently without eating. We are wandering about like half starved wolves and no person appears to know in what direction we ought to steer . . .

The second is the reconnaissance of the Des Moines River watershed

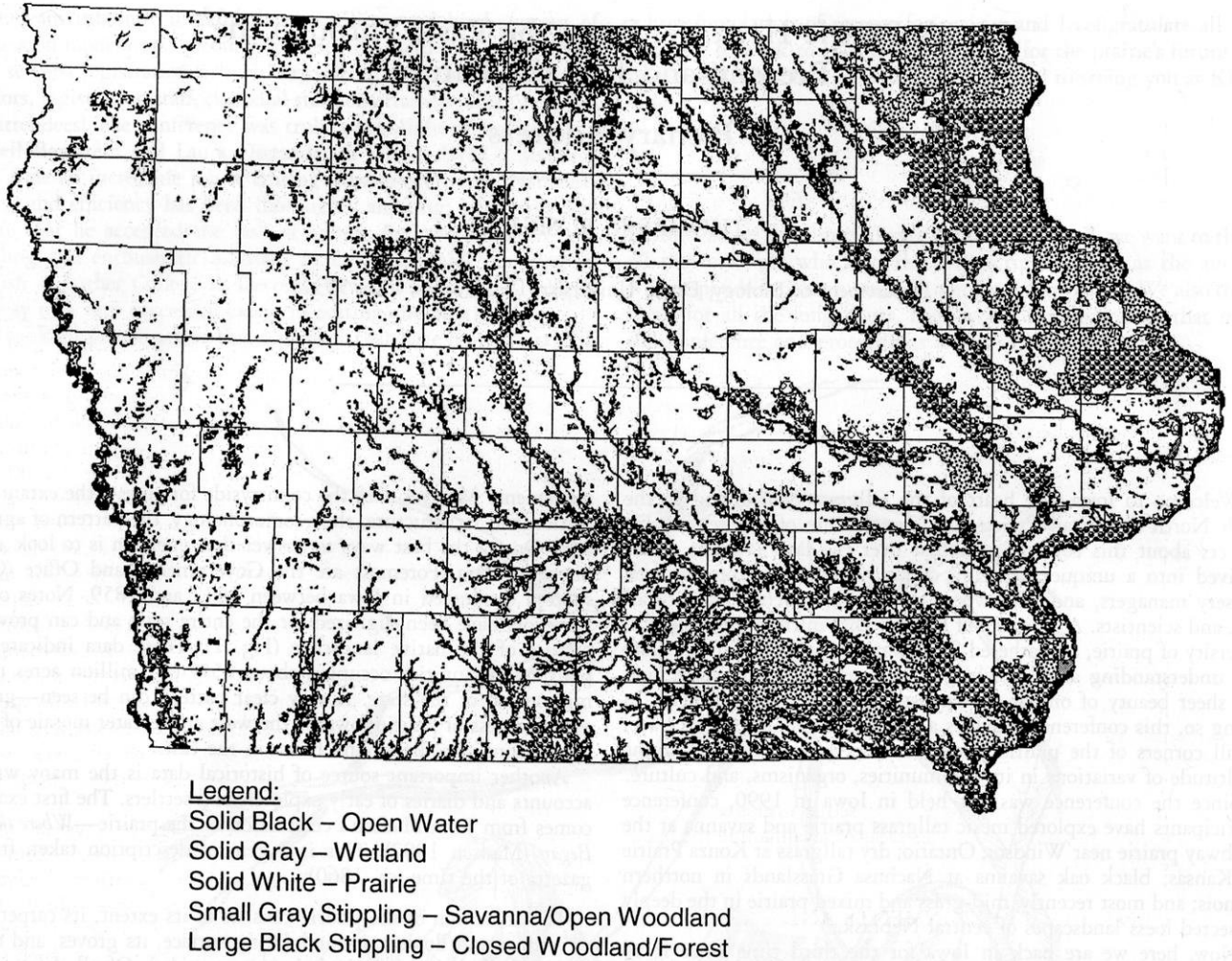


Fig. 1. Presettlement vegetation as determined by Government Land Office surveys between 1832 and 1859 (from Anderson 1996).

by Allen (1845), which followed a route through north-central, northwest, and west-central Iowa:

... many wet places to detain the wagons ... left the Des Moines far to our right; prairie large and flat, running up close to the river, where it falls off in a sudden bluff, serrated with deep short ravines, with good springs ... saw many elk at a distance; one drove estimated at 100 ... beautiful prairie all around and extending to the Des Moines ... we had to double the teams, and also apply the men to draw the wagons through the slues, and these were numerous ... We spent the whole of this day in fruitless search of a way to lead us through these interminable lakes ... The grass of this country is tall and luxuriant ... but the whole of this country is good for nothing, except for the seclusion and safety it affords to the numerous water fowl that are hatched and grown in it ... Buffalo have been in sight almost always since we struck this river [Big Sioux in northwest Iowa], and we might have killed hundreds by delaying for the purpose ... Met another ugly prairie slue at the end of eight miles, which took three hours to cross, when we came to a country full of marshes and old shallow grass ... four fifths of the country was marsh, which turned us to all points of the compass ... encamped on the open prairie; no timber near us ...

The last example includes a few excerpts from a report published in 1852 and prepared by C. C. Parry, a medical doctor who accompanied the geologist David Owen on an expedition into the upper Mississippi River Valley. Parry provided brief comments on the plants he collected (Owen 1852):

Ceanothus Americanus, (L.) July. "Red root." A shrubby plant, well known on the Iowa prairies as a troublesome obstacle, by its tough roots in first breaking the soil ... *Astragalus caryocarpus*, (Ker.) May. Gravelly ridges in the interior of Iowa, Fort Snelling, at the junction of the Mississippi and St. Peter's Rivers, and abundant on the later stream, being a characteristic plant of the peculiar drift deposit of that region. The fruit, which is a pod, closely resembles a plum in external appearance, from which fact it has received the common name "ground plum." The thick fleshy exterior is highly charged with moisture, having the usual taste of the pea tribe, and is frequently used to allay the thirst of the traveler on the great western plains ... *Onosmodium molle*, (Michx.) About gopher holes, on prairie. Iowa and Minnesota ... *Asclepias Meadii*, (Torr.) June. Of a singular isolated habit, but not rare on dry rolling prairies. Iowa.

A third measure of the historical landscape is provided by photos

and illustrations. Lacking cameras, geologists relied on sketches as a method to record landscape features. Orestes St. John, an assistant to the geologist Charles White, worked throughout Iowa recording the details in the native landscape. His illustration of Flint Creek in Des Moines County (southeast Iowa) shows limestone outcrops with a savanna-like community evident along the bank (Fig. 2A). Another sketch made about 2 miles north of Clear Lake shows a wetland (peat marsh) surrounded by knob and kettle terrain with scattered trees to the southwest and more open prairie to the north (Fig. 2B), and a third sketch illustrates the Loess Hills in Plymouth County north of Sioux City. The Big Sioux River floodplain is on the left and has a few scattered trees present, but the bulk of the Hills are treeless (Fig. 2C).

The best these historical descriptions can do is give us an impression of the physiognomy, that is the basic appearance of the landscape. Finer scale historical descriptions, for example, of specific community types, are pretty much non-existent. For a map of more specific presettlement communities, we can turn to a description of the soils.

Vegetation is a principal soil-forming factor, and the type of vegetation present (historically) during soil formation imparts certain characteristics in the soil. By using the descriptions in soil surveys, an association between a soil series and a prairie community, such as wet, mesic, or dry tallgrass, can be made, although it is somewhat subjective and of course contains no information on specific plant species composition. For example, the soil map for Story County, Iowa (DeWitt 1984) shows more specifically the types of prairie on two sections of land north of Ames (Fig. 3). Including the two wetland communities, there are seven plant communities that can be differentiated on this prairie landscape on the basis of soil characteristics. The landscape was a mosaic of wet-mesic and mesic tallgrass prairies with a few potholes and possibly sedge meadows (the wet prairie). Dry tallgrass and some small areas of savanna line the banks of a prairie stream.

PRESENT DAY ENVIRONMENTS AND PRAIRIE

To really understand the patterns of community composition across a landscape, we first need to recognize the environmental factors affecting the species. For any vegetation, and grasslands are no exception, geology and climate are a good place to start. Let's first consider geology and geomorphology.

Iowa's bedrock record is primarily sedimentary (mostly limestone) and ranges from 75 to 500 millions years old (Prior 1991). The youngest bedrock deposits are Cretaceous (found in the northwest), then Pennsylvanian (in the southwest) and Mississippian, Devonian, Silurian, Ordovician, and a little bit of Cambrian in the northeastern corner of Iowa. A cross section from northeast to southwest would show that the bedrock tips downward, so that as one moves towards the northeast, progressively older rocks outcrop on the surface.

More important in terms of soils and geomorphology is the record of glaciation during the Pleistocene. All of Iowa had several layers of glacial drift deposited between 500,000 years ago and the beginning of the Pleistocene about 2.5 million years ago (Prior 1991). The next wave of glaciation, about 130,000 to 300,000 years ago, had little impact on Iowa—touching only a small portion of south-east Iowa along the Mississippi River. The most recent glacial deposits were left just 10,000 to 30,000 years ago in north-central Iowa.

Iowa's bedrock and the glacial activity combine to distinguish eight principal landform regions (Fig. 4): Des Moines Lobe, Iowan Surface, Paleozoic Plateau, Mississippi and Missouri Alluvial Plains, Southern Iowa Drift Plain, Loess Hills, and the Northwest Iowa Plains (Prior 1991). Let's take a closer look at some of these major

landforms, since they have a primary influence on the soils formed and therefore the variation in prairies across the state.

The Des Moines Lobe is a young landscape with fresh glacial drift (10,000 years old). Much of the area has level terrain with poor surface drainage, which results in a range of wet prairies grading to wetlands. Morainal deposits along edges of the stagnant ice sheet resulted in "knob and kettle" terrain, which provides a modest amount of topographical relief and usually very porous deposits, such as gravel outwash, that are characteristically gravel hill prairies. The Southern Iowa Drift Plain is characterized by a moderate amount of loess lain like a blanket over very old glacial drift. Ongoing development of surface drainage (i.e., a dissected terrain with river and stream valleys) has removed the loess from side slopes exposing paleosols (which are ancient soils) formed in the top of the glacial drift. The paleosols contain high amounts of clay and form an impervious layer, which can cause perched water tables and side hill seeps.

The Iowan Surface is essentially the Southern Iowa Drift Plain but with a major erosion event that occurred during the maximum cold of the Wisconsin glacial advance about 16,000 to 21,000 years ago. It left a landscape reduced in topographical relief with a thin, discontinuous layer of loess over top old glacial drift. An erosion-resistant stone or cobble line is also characteristic. Toward the southern part of the Iowan surface, paha ridges occur. These long narrow ridges, which are mostly aligned northwest to southeast, appear to be formed from windblown silt and sand. These dune-like formations protected and preserved the pre-erosion landscape below them. The Paleozoic Plateau has a thin layer of loess with scattered patches of glacial drift over bedrock. It is a bedrock-dominated landscape with deeply entrenched river valleys. Considerable topographic relief is associated with the valleys. Karst topography (which gives rise to a network of caves and sinkholes) is also characteristic. Steep slopes and thin soils promote dry prairie vegetation.

Finally the Loess Hills are formed from very deep, up to 200 feet thick, deposits of loess (windblown silt). Glacial outwash from melting ice sheets to the north was carried down the Missouri River and deposited on the adjacent floodplain. Silt was blown from the floodplain into huge drifts that were eroded into a network of steep interconnected ridges and valleys. The high topographic relief, southwestern slope exposures, and steep slopes contribute to very dry microclimates.

Most travelers passing through Iowa probably remember the Iowa landscape as pretty flat and uninteresting, but there really is a fair amount of edaphic, geomorphological, and topographical variation if you know where to look. These variations in landform, even though relatively subtle by some standards, create environments that proliferate Iowa's prairie diversity. They contribute to microclimates that effectively stretch the moisture gradient to impressive lengths—from the super-saturated fens and sedge meadows moistened by geological deposits and topographical basins, to the rapidly permeable sand prairies colonizing aeolian deposits along the margins of large river valleys and the bone-dry prairie on thin soils of bedrock-strewn slopes or clinging to steep loess ridges. Become familiar with Iowa's landforms, and you will have taken a giant step forward in understanding Iowa prairie.

There are several important climatic patterns that add a layer of variation to Iowa's prairie environment. Annual precipitation varies from less than 71 cm (28 inches) in the northwest to 96 cm (38 inches) or more in the southeast (Fig. 5). Temperature patterns indicate that cold air invades Iowa pretty uniformly from the north (Fig. 6). Average January lows in the north are about -15°C (5°F) while lows in the south are about -11°C (12°F). However, the maximum cold temperatures vary by 12°C (-40°C in the north and -28°C in the south). The pattern in the July high temperatures indicates hot air enters Iowa from the southwest. Southwestern Iowa

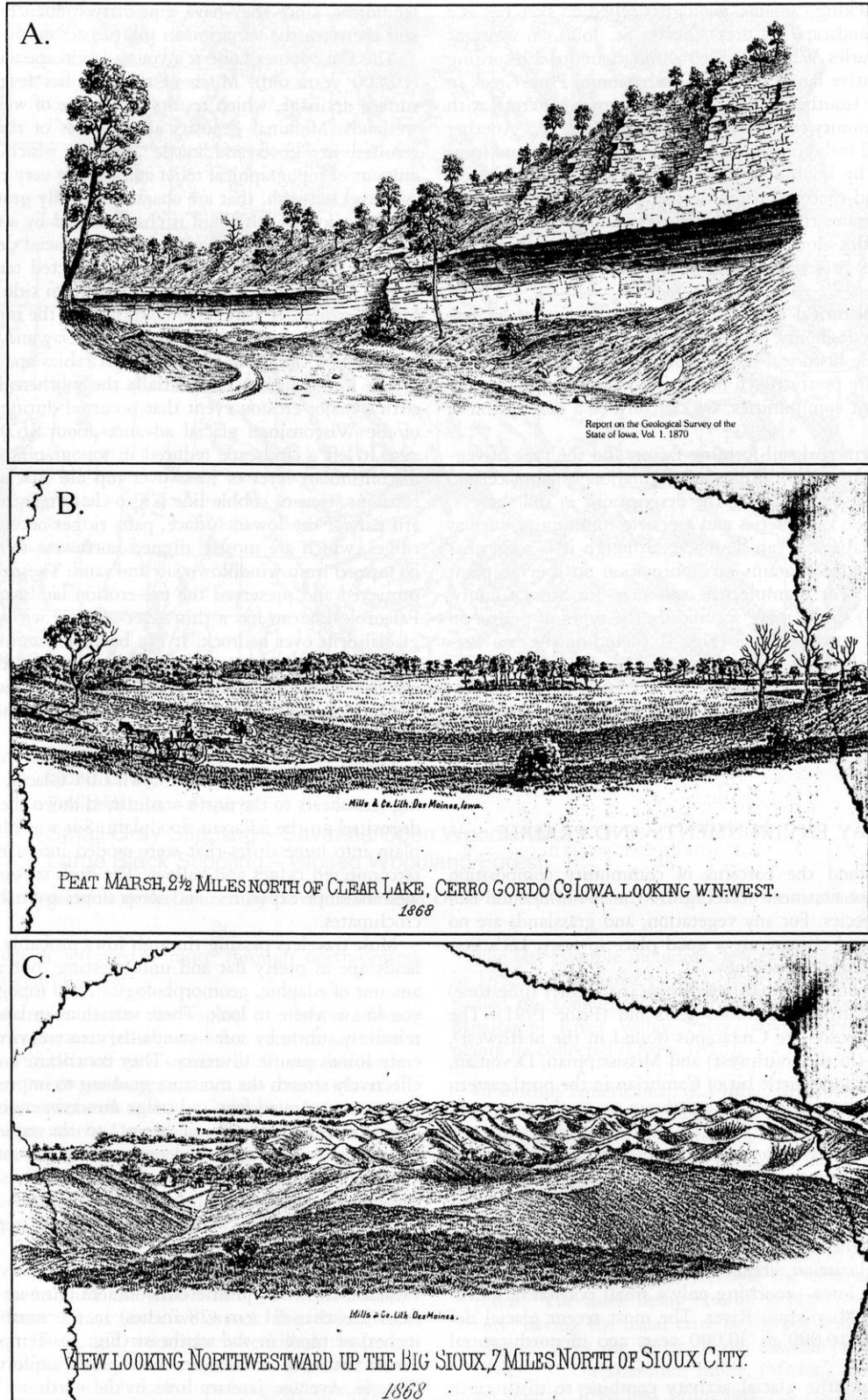


Fig. 2. Landscape sketches of selected counties in Iowa by Orestes St. John (from White 1870).

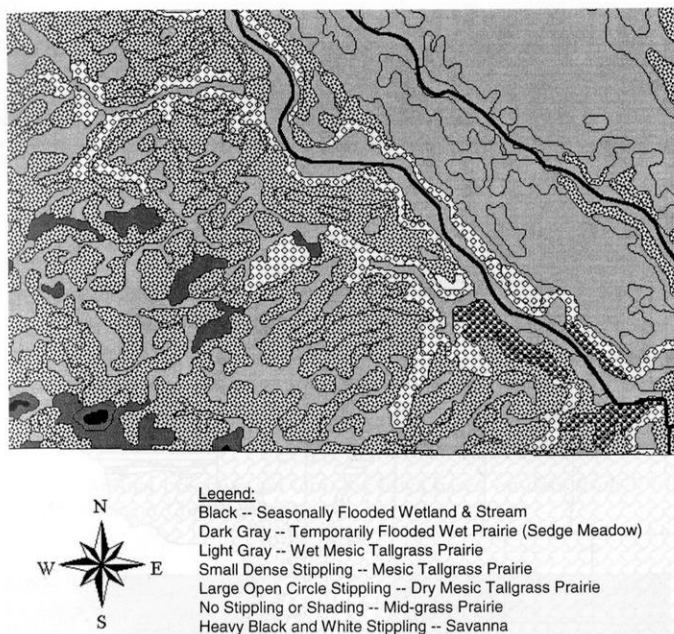


Fig. 3. Presettlement vegetation on two sections of land in northern Story County, Iowa, based on soil series maps (DeWitt 1984).

experiences average July highs of 31°C (88°F), while northeastern Iowa is about 3°C cooler at 28°C (82°F). Maximum high temperatures are fairly uniform over the state at about 43°C (110°F). The exception is northeastern Iowa where they are 5°C cooler. These temperature differences across the state translate to about a 27-day shorter growing season in the north (135–150 days) than in the south (165–175 days) (Eilers and Roosa 1994).

Wind speeds are greatest in the northwest and are generally higher across northern Iowa (Fig. 7). Lowest wind speeds occur in the southeastern third of the state and especially in the Paleozoic Plateau adjacent to the Mississippi River in northeastern Iowa. Wind has a major influence on increasing evapotranspiration and contributing to water stress, and also to increasing fire intensity and spread.

If the effect of river valleys as fire barriers is added, it becomes clear that with prevailing southwestern or southerly winds during the fire season, the fire frequency and intensity would be much lower in eastern Iowa than in the west and northwest. In the east there are many large river valleys oriented in a northwest to southeast direction that are generally perpendicular to the prevailing wind direction and the spread of fires. These natural firebreaks combined with lower wind speeds would have created a more patchy and random pattern of fire on the landscape in the east, which contributes to greater occurrence of savanna and woodland communities. By contrast, the rivers in the western third of the state flow from northeast to southwest and therefore form valleys that generally do not function as effective fire barriers.

With some understanding of the variation in the physical environment, prairie ecologists can begin to construct a picture of how these factors (and others) affect the species composition of Iowa prairie. In one of the earliest attempts to make sense of Iowa prairie, Shimek (1911) described six basic community types: 1) the flat prairie (the wet to wet-mesic, black soil prairie in much of the Des Moines Lobe), 2) the rolling prairie (mesic to dry-mesic throughout the Southern Iowa Drift Plain), 3) the western ridges (dry prairie in the Loess Hills), 4) the alluvial prairie (wet and wet-mesic prairie in floodplains), 5) the prairie openings (dry-mesic prairie, or savanna,

on ridges in eastern Iowa), and 6) the sand-dunes (sand prairie associated with river valleys).

More recently, the best quantitative descriptions of prairie communities have come from ecological work on remnants. Three landscape-level studies on the community ecology of prairie have been completed in Iowa. White (1983) focused on many of the prairies throughout the state that are within the state preserve system. He observed 138 community samples from nine locations in Iowa and two in southeastern Nebraska. Ugarte (1987) confined his work to the northeast Iowa hill prairies. He included 174 samples in his data set. Rosburg (1994) studied 250 samples from nine locations in the Loess Hills.

The community types described by each are arranged from top to bottom in increasing order of soil moisture (Table 1). All of them, except the last four described by White (1983), represent prairies on the dry side of the moisture gradient. Because White's samples embody much of the Iowa landscape, these types epitomize the bulk of the original prairie in Iowa. Wet, wet-mesic, mesic, and dry-mesic tallgrass are well represented in Iowa. White's Iowa Erosion Surface (now called the Iowan Surface) mesic tallgrass is characterized by several forbs that have a biogeographical range limited to northeastern Iowa, which distinguishes the prairies on the Iowan Surface from other tallgrass prairies.

Ugarte's (1987) four community types on the Paleozoic Plateau are mostly distinguished by relative elevation and the level of recent grazing activity (the more intense the grazing the more dominance by mid-grass species like little bluestem and side-oats grama). All occur on thin soils associated with steep, bedrock-dominated slopes.

In the Loess Hills, much of the remnant grassland is mid-grass prairie represented by Rosburg's (1994) first three types. These occur on the very steep bluffs adjacent to the floodplain and on west- or south-facing slopes at high relative elevation throughout the Hills. Tallgrass species mix equally with mid-grass species in the tall/mid-grass transition, which can be found on northwest and southeast facing slopes. Dry-mesic tallgrass is found on all slopes at medium to low relative elevations.

In order to learn more about dry prairie in Iowa, I combined the field data from all three studies (excluding White's mesic to wet types) and did an analysis of the variation in community composition using ordination techniques. An ordination shows relative levels of similarity among samples (in this case, the community types of each study) by plotting them in two-dimensional species space. The closer two samples are in the ordination, the more similar they are in species composition. Abundance was measured in two ways—one by relative cover or frequency and the second by presence/absence in community samples (this is called constancy). If abundance of species is based on cover or frequency measurements, then grasses tend to have a higher relative abundance than forbs and essentially weight the community composition more towards the grasses (Fig. 8A). In this case, the dry-mesic tallgrass types group together towards the top left, all the mid-grass types (including the gravel hill which is a mid-grass community) group together towards the bottom left, and the sand prairie is very distinctive, located on the right side and separated from all the others. When grasses are given a lot of weight in the analysis, biogeography has little effect—loess mid-grass communities are more similar to gravel hill and northeast Iowa hill prairies than they are to loess hill tallgrass communities. There is good separation of tall grasses (big bluestem and indiagrass) and mid-grasses (little bluestem and side-oats grama) along a presumed moisture gradient (axis 2, Fig. 8A).

In the second ordination, abundance was based on constancy, and consequently forbs were given relatively more weight (Fig. 8B). This changes the outcome considerably. Now all of the Loess Hill communities group together as do the northeast Iowa hill prairies. Dry-

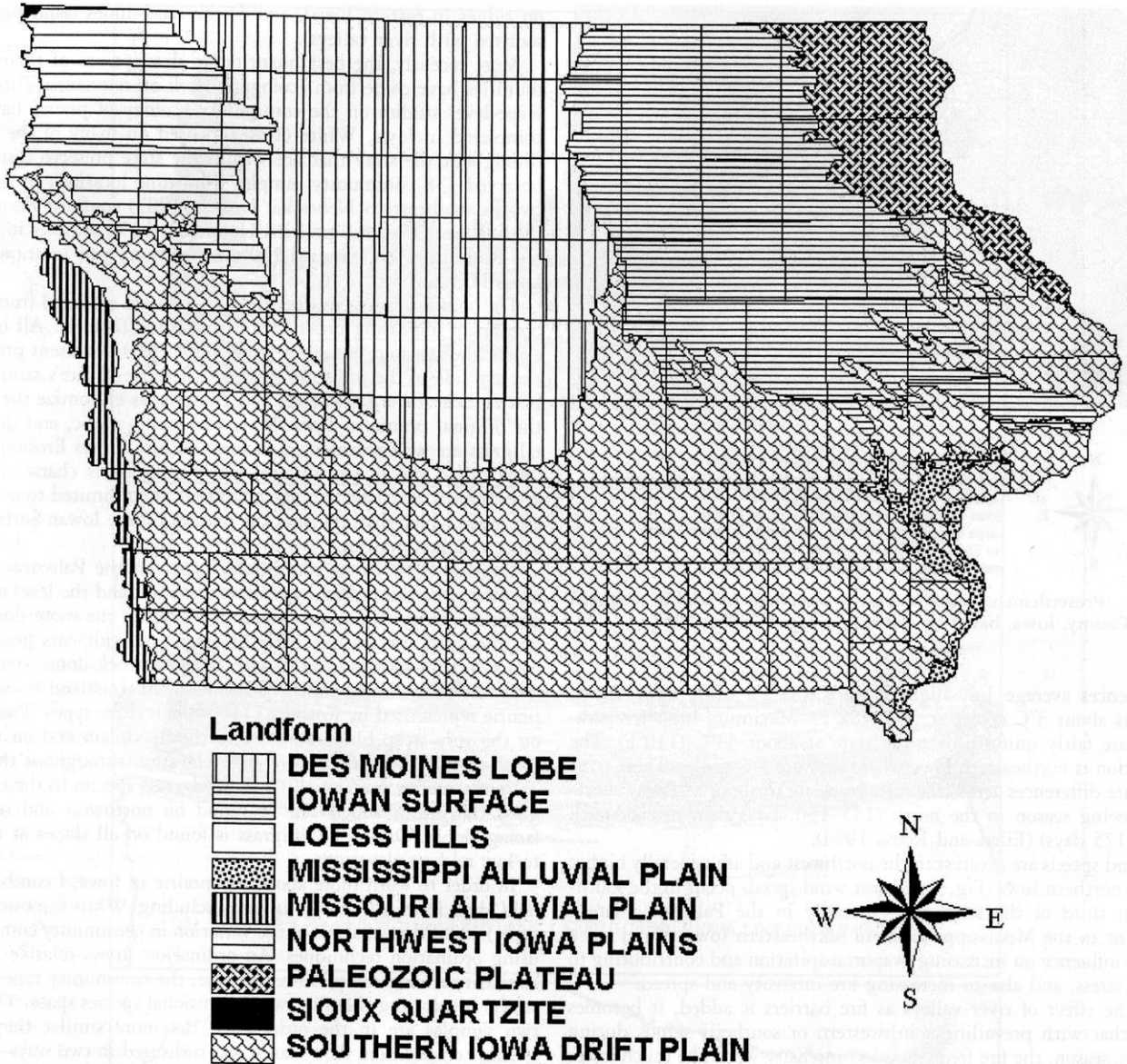


Fig. 4. Landform regions in Iowa (Prior 1991).

mesic tallgrass and gravel hill are fairly similar and form their own group. Sand prairie is still distinctive, but not as much, and it is surprisingly most similar to the southeast Nebraska samples. The lesson here is that although grasses certainly make a major contribution to the productivity and structure of a prairie, the species are fairly uniform within broad physiognomic grassland types. It is the forbs—with their own specific patterns of biogeography and habitat requirements—that reflect variation in species composition and make a potpourri of community types across the prairie landscape.

A three-dimensional model of Iowa prairie integrates the three principal and independent environmental factors affecting species composition of prairie communities and provides a mechanism for visualizing the prairie's complexity (Fig. 9). The three main environmental gradients are soil moisture/fertility, biogeography, and frequency of environmental perturbation. Soil moisture/fertility is the primary gradient. It segregates the prairie into the community types most commonly recognized (e.g., wet, mesic, dry). However, com-

munity types are arbitrary entities. In some cases, wet vs. mesic vs. dry may be good enough, but in other situations, more resolution of prairie communities may be desirable. The additional resolution comes from accounting for variation in species composition due to the effects of the other two gradients—biogeography being the second most important and environmental perturbation the third most important.

For each of the gradients depicted, several different environmental factors can affect species composition via the environmental gradient. For example, the soil moisture/fertility gradient can be influenced by at least five factors. Deep and/or fine-textured soils, low relative elevation, northeast slope exposures, and southeast Iowa weather all would nudge a prairie more towards the wet end of the moisture gradient.

The biogeography gradient is directly affected by variation in latitude and longitude and can be indirectly related to species responses to climate patterns, the location of species origin, and the location

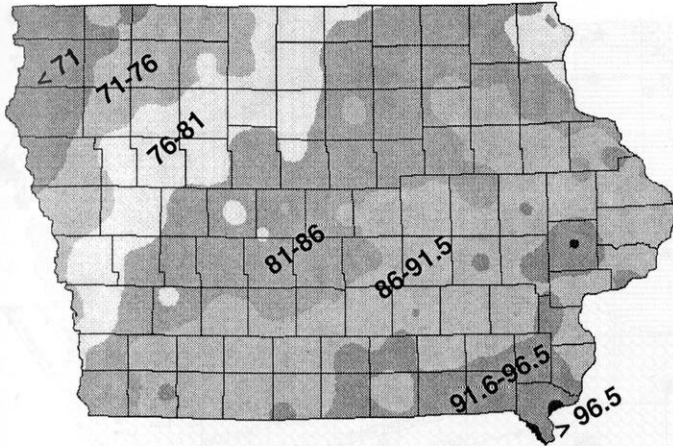


Fig. 5. Annual precipitation (cm) for Iowa based on data from 1961 to 1990 (Oregon Climate Service).

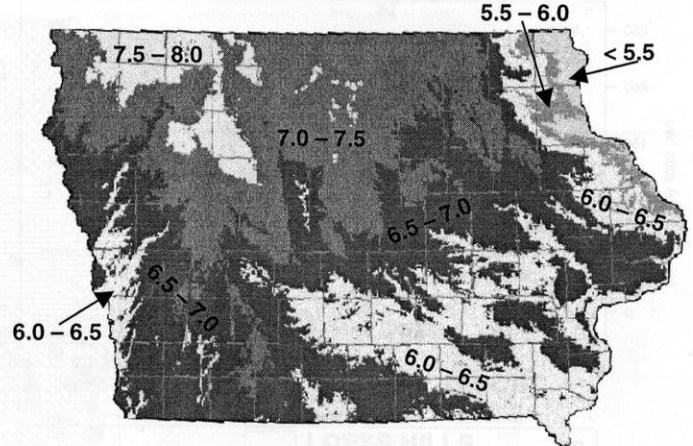


Fig. 7. Average wind speed (m/s) across Iowa (Iowa Energy Center 1997, reprinted with permission).

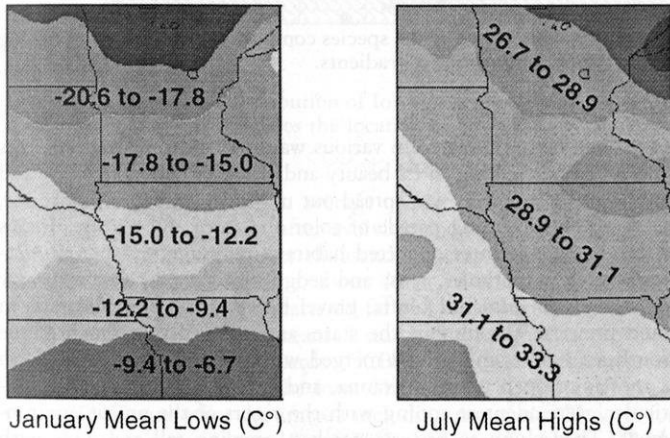


Fig. 6. Iowa 30-year normals for January minimum and July maximum temperatures (High Plains Regional Climate Center).

of species refugia during the Pleistocene glacial stages. Species biogeography is especially important because Iowa is in the heart of the tallgrass prairie, and therefore species reach into Iowa from all corners of the grassland biome.

The third gradient incorporates the effects of perturbation, that

is, factors that occur in a discrete portion of time and space and which cause changes in resource availability and species interactions through increased stress or mortality. If mortality occurs to the extent that space becomes available for colonization and establishment, the term disturbance is applied by ecologists. For example a perturbation may result from frequent spring burning, as some research indicates that after many years of annual spring burns the warm-season grasses become more dominant while the forbs becomes less diverse and abundant (Gibson and Hulbert 1987). The context of the perturbation is extremely important; Henderson (1992) found that in dry prairie ten years of annual spring burning did not cause as much change as one year of drought, and any change in composition that did occur due to annual spring burns was mostly reduction in cool-season graminoids and not the loss of spring forb abundance and diversity. Another perturbation is moderate grazing, which increases forb diversity by favoring the abundance of low-stature and basal-leaved species like blue-eyed grass, wild flax, and violets (Rosburg 1994). Platt (1975) demonstrated that gopher and badger mounds are soil disturbances that provide important habitat for a group of prairie forbs.

The three-dimensional volume represents all of the potential variation in species composition of Iowa prairie, thus a single prairie community type occurs in a subset of the volume. Its place in the volume (i.e., its x, y, z coordinate) represents the contribution from each gradient. For example, savanna communities would occupy only a portion of the total volume. At the biome scale, climate is an

Table 1. Iowa prairie community types identified by studies incorporating quantitative field methods and multivariate classification.

White 1983 Des Moines Lobe Iowa Erosion Surface Southern Iowa Drift Plain	Ugarte 1987 Paleozoic Plateau	Rosburg 1994 Loess Hills
Sand	Overgrazed Mid-grass	Bluff Mid-grass
Gravel Hill	Mid-grass	Dry Mid-grass
Dry-Mesic Tallgrass	Dry-Mesic Tallgrass	Mid-grass
Mesic Tallgrass	Ungrazed Tallgrass	Tall/Mid-grass Transition
Wet-Mesic Tallgrass		Dry-Mesic Tallgrass
Iowa Erosion Surface Mesic Tallgrass		
Wet Tallgrass		

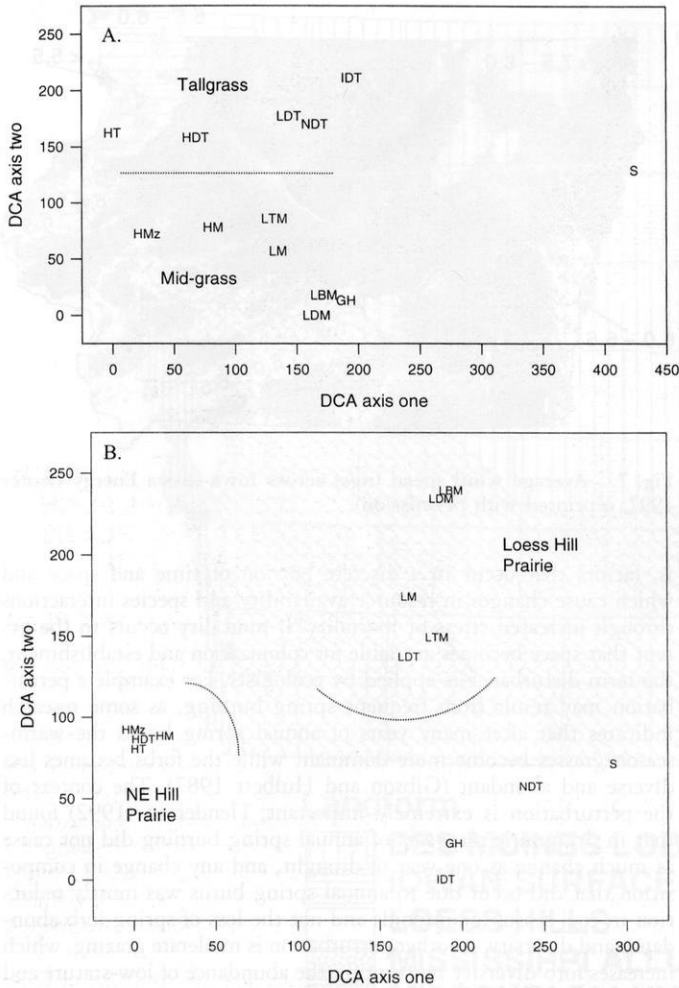


Fig. 8. Ordination of Iowa dry prairie community types using either A) cover or frequency measurements or B) constancy measurements (from Rosburg 1999). Data points represent the average composition of samples within community types. Community types described by White (1983) include: Sand (S), Gravel Hill (GH), Iowa Dry Mesic Tallgrass (IDT), and Southeast Nebraska Dry Mesic Tallgrass (NDT). Northeastern hill prairie types described by Ugarte (1987) include: Ungrazed Tallgrass (HT), Dry Mesic Tallgrass (HDT), Mid-grass (HM), and Overgrazed Mid-grass (HMz). Community types in the Loess Hills identified by Rosburg (1994) include: Bluff Mid-grass (LBM), Dry Mid-grass (LDM), Mid-grass (LM), Transitional Tall/Mid-grass (LTM), and Dry Mesic Tallgrass (LDT).

important environmental factor; wet climates with infrequent droughts promote low fire frequency and increased woody growth present in a savanna. Fire frequency is also affected by several local factors. Thin soils, which have low productivity and fuel loads; low relative elevation, which promotes wet fuel loads; and northeast slope exposures all would tend to decrease fire frequency and intensity, thereby promoting the development of savannas and/or oak grubs. There is also good reason to factor in the browsing effect of large ungulates like bison and elk because greater browsing intensity helps to promote savanna instead of forest by stressing woody species along forest edges where encroachment begins.

So the question still lingers. Can we ever really gain full appreciation of the original Iowa prairie landscape? We certainly know that it was a complex system, affected by many different factors,

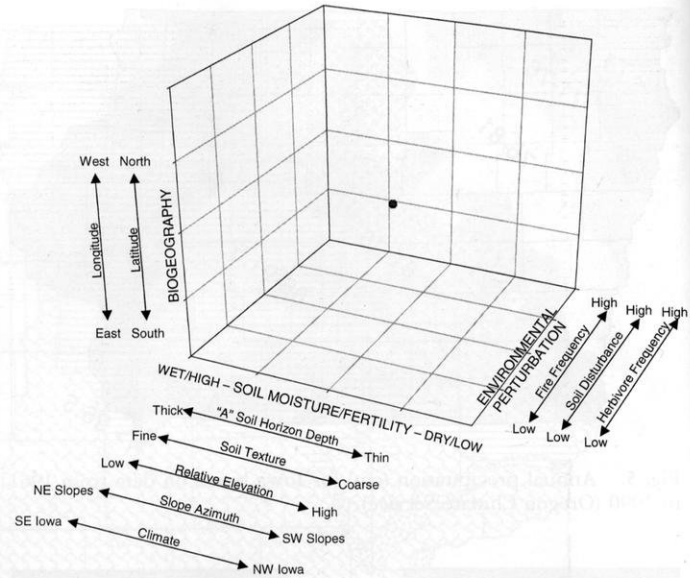


Fig. 9. Factors affecting the species composition of Iowa prairie along three major compositional gradients.

many of which interacted in various ways. A landscape that at times was loud and striking in its beauty and, at other times, secretive and subtle in its mood. It was spread out under an immense prairie sky, a seemingly unending parade of color and form and texture. It was a vast mosaic of interconnected habitats, ranging from prairie wetlands such as potholes, fens, and sedge meadows to extremely dry grasslands on loess hill bluffs, gravel hill prairies, and blowouts in sand prairies. Throughout the state, and especially in much of the southeast half, it mixed and merged with fire-tolerant trees to form a mosaic of open prairie, savanna, and woodland. Bur oaks, in particular, were adept at coping with the rigors of the prairie environment. They clung to fire-safe patches, growing tall and wide with gnarled and twisted branches reaching widely to all corners of the sky.

Some plants were fussy, preferring to stay in certain sections of the state. Northern blazingstar and plains milkvetch only occur across the northern sections; eastern species include feverfew and shooting star; ironweed and purple coneflower were confined to the southern part of the state, while purple locoweed and prairie turnip creep into Iowa from the west.

It was full to the brim with life of all shapes and forms and colors, animals like ladybird beetles, ambush bugs, short-horned grasshoppers, sphinx moths, skippers, and crab spiders; larger critters like leopard frogs, toads, fox snakes, and yellow-bellied racers. Prairie chickens were so numerous that hundreds could be killed by a single hunter in one day. Now they are making a comeback in southern Iowa's prairie pastureland. Many other prairie birds filled the sky with their song, species like upland sandpipers, bobolinks, and dickcissels. Among the mammals, prairie voles scurried through tunnels in the prairie thatch, badgers plowed through the prairie soil close on the heels of fleeing ground squirrels, elk wandered half hidden amid tall grasses and forbs, and bison herds, forever seeking the open spaces, thundered across the prairie.

It was a glorious landscape indeed. Nothing else on earth was like it. And then we came along and life on the Iowa prairie was forever changed. It's hard to believe that so much could be destroyed so fast. By 1850, just four years after statehood, settlement had already encompassed the entire southeastern corner of the state. By 1890 Iowa,

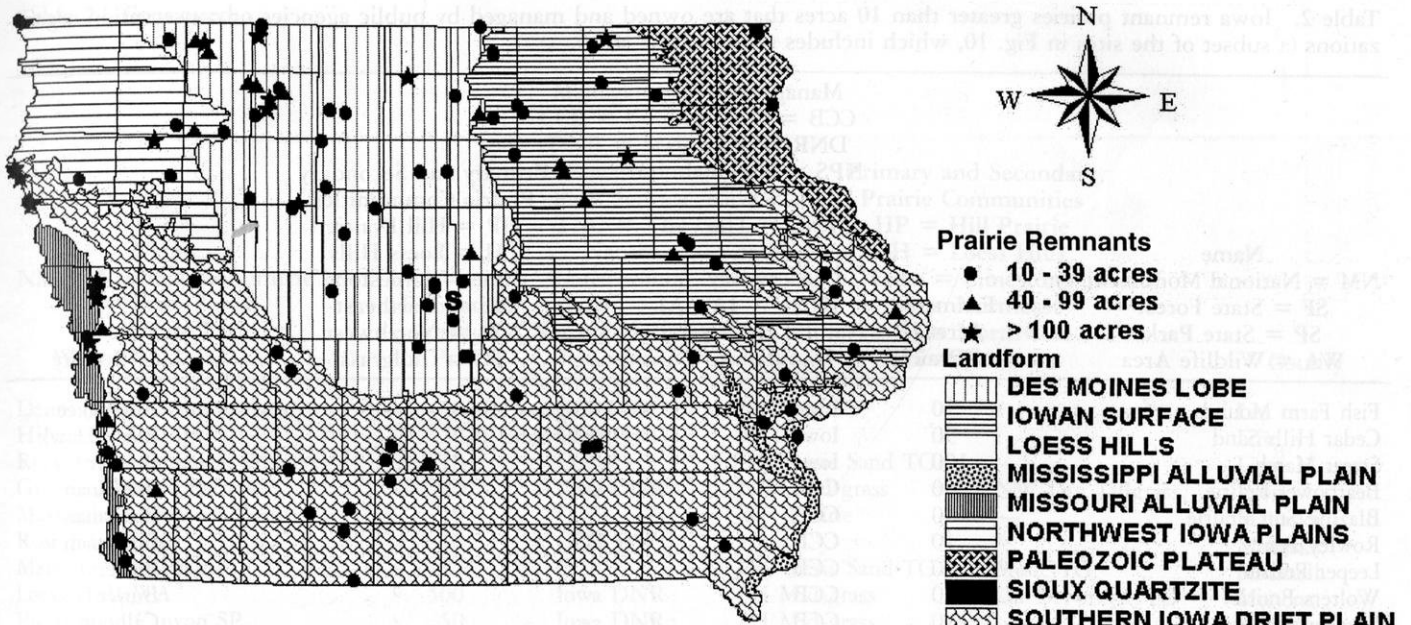


Fig. 10. Location and distribution of Iowa prairie remnants 10 acres or more in size. Data were compiled from a variety of public and personal data sources. The "S" indicates the location of Story County.

was declared settled, with an average of four farms per square mile (Smith 1992). The prairie, after evolving and having become more complex and refined for over thousands of years, was destroyed in less than one person's lifetime, about 40 to 50 years.

What's left? Just slivers scattered far and wide, barely perceptible amid the flood of corn and beans. I searched through data provided by County Conservation Boards (CCBs), the Iowa Department of Natural Resources (DNR), the Iowa Chapter of The Nature Conservancy (TNC) and other documents including my own field notes for remnants that were at least 10 acres (4 ha) in size (Fig. 10 and Table 2). This is not a complete data set—there are certainly many more privately-owned remnants, especially in the Loess Hills, and also probably in the Paleozoic Plateau and Southern Iowa Drift Plain. There are also many more remnants that are less than 10 acres (4 ha) in size. Nevertheless, current estimates place the amount of surviving prairie at between 0.07 and 0.1% (or between 20,000 and 30,000 acres) (8,093 and 12,140 ha). The bulk of this, perhaps as much as 15,000 acres (6,070 ha), occurs in the Loess Hills. Among this sample of 120 remnants, 70% are between 10 and 40 acres (4 and 16 ha), 15% are between 40 and 100 acres (16 and 40 ha), and 15% are over 100 acres (40 ha). The largest contiguous tracts, upwards of 1,000 acres (405 ha), are found in the northern Loess Hills at Broken Kettle Grasslands, owned and managed by the Iowa TNC. In terms of management, just over half (52%) are managed by CCBs, 19% are privately-owned, and 18% are managed by the Iowa DNR (mostly by wildlife management biologists). The remaining caretakers include Iowa TNC, Township Trustees, the Iowa Natural Heritage Foundation, and the National Park Service.

While these data serve to show the distributional pattern of significant extant prairie tracts in Iowa, they do not show the entire picture. If all prairie tracts of an acre or more in size are included, for example in Story County, the number of remnants goes from four (Fig. 10) to 30, and the percentage of privately-owned sites increases dramatically. Seventeen of the 30 (57%) of these are privately-owned, six are owned by the CCB, five are cemeteries, and one each is owned by TNC and the Iowa DNR. Three occur along abandoned railroad

lines. They vary in quality from barely passable as a remnant to one that has a population of a federally endangered plant species. This strikes me as a fairly impressive number of remnants, and I doubt that it is complete. There may be one or two that I'm missing. I'd like to think that other counties have similar numbers, but I wouldn't be surprised to learn that there are counties with virtually nothing left. Still, you can never be sure until a thorough survey is completed.

Now let's take a quick tour across the state to see some of these remnants, starting in central Iowa. Doolittle Prairie, just north of Ames, is a state preserve managed by the Story CCB. It's a good example of a prairie remnant on the Des Moines Lobe, where wet and wet-mesic prairie are interspersed with scattered potholes. Blue flag is occasionally found in the wet prairie along with Virginia mountain mint and sneezeweed. In the more wet-mesic areas, you can find butterfly milkweed, New England aster, and purple meadow rue. Elsewhere in the Des Moines Lobe, mesic and dry-mesic prairies occur on gentle slopes associated with stream valleys, like Pohl Prairie in Ames, a state preserve managed by TNC. It's a good place to see plants like prairie gentian, prairie rose, and prairie dandelion. In the northwest corner of the Des Moines Lobe, nestled in the knob and kettle terrain associated with the western moraine, you'll find Freda Hafner Kettlehole and Cayler Prairie, both of which are state preserves. Lowlands are wet-mesic prairie with golden alexanders and Canada anemone, while ridges at Freda Hafner are gravel hills mid-grass prairie and are good places to run into a prairie skink or see clumps of Junegrass and the vibrant color of aromatic aster. In general, the gravelly deposits of the glacial moraines have thin, nutrient-poor soils and are also good places to look for diminutive species like the Carolina anemone. The knob and kettle terrain is also a good place to find prairie fens. These unique habitats are home to many great plants, including white lady slipper orchids, bog twayblade, fringed gentian, and fen endemics like grass of Parnassus.

A gem on the Iowan Surface is Hayden Prairie, another state preserve owned and managed by the DNR. Hayden is 240 acres (97 ha) of delightful prairie. If your timing is right, you might see

Table 2. Iowa remnant prairies greater than 10 acres that are owned and managed by public agencies or conservation organizations (a subset of the sites in Fig. 10, which includes some private sites).

Name	Estimated Acreage of Prairie	Management CCB = County DNR = State NPS = National Park Service TNC = The Nature Conservancy INHF = IA Natural Heritage Foundation	Primary and Secondary Prairie Communities HP = Hill Prairie LH = Loess Hills Lime = Limestone NE = Northeast NW = Northwest TG = Tallgrass	County
Fish Farm Mounds	10	Iowa DNR	NE Mid-grass HP	Allamakee
Cedar Hills Sand	90	Iowa TNC	Dry-mesic Sand TG	Black Hawk
Sweet March	100	Iowa DNR	?	Bremer
Bearbower Prairie	40	CCB	?	Buchanan
Blazing Star Prairie	10	CCB	?	Buchanan
Rowley Fen	10	CCB	Wet TG	Buchanan
Leeper Prairie	40	CCB	?	Butler
Wolters Prairie	40	CCB	?	Butler
Munson Prairie	10	CCB	?	Calhoun
Rochester Cemetery	15	Township	Mesic TG	Cedar
Blazingstar Prairie	10	CCB	Wet-mesic TG	Cerro Gordo
Hoffman Prairie	35	Iowa TNC	Wet-mesic TG	Cerro Gordo
Walch WA	50	CCB	?	Cerro Gordo
Nestor Stiles Prairie	10	CCB	Mesic TG	Cherokee
Steele Prairie	200	Iowa DNR	Mesic TG	Cherokee
Joachim Prairie	25	CCB	?	Chickasaw
Coyote Canyon WA	10	CCB	?	Clarke
Bertram Reservation	50	CCB	Dry-mesic TG	Clay
Burr Area	30	CCB	Oak Savanna	Clay
Dewey's Pasture	50	Iowa DNR	Wet-mesic TG	Clay
Effigy Mounds NM	20	NPS	NE Mid-grass HP	Clayton
Duke Prairie	20	CCB	Mesic TG	Clinton
Manikowski Prairie	40	CCB	Dry-mesic Lime TG	Clinton
Newcom Prairie	10	CCB	Dry-mesic TG	Crawford
Cayler Prairie	150	Iowa DNR	NW Wet-mesic TG	Dickinson
Dugout Creek WA	50	Iowa DNR	NW Dry-mesic TG	Dickinson
Freda Hafner Kettlehole	75	Iowa TNC	NW Mid-grass	Dickinson
Anderson Prairie	200	Iowa DNR	NW Wet-mesic TG	Emmet
Eagle Lake Wildlife	20	Iowa DNR	?	Emmet
Rockford Fossil Park	20	CCB	?	Floyd
Creeden Prairie	10	CCB	?	Franklin
Waubonsie SP	20	Iowa DNR	LH Mid-grass	Fremont
Scheueman Prairie	15	CCB	Wet-mesic TG	Greene
Sheeder Prairie	25	Iowa DNR	Mesic TG	Guthrie
Crystal Lake	100	CCB	?	Hancock
Hubbard Prairie	50	CCB	Mesic TG	Hardin
Loess Hills SF-west	150	Iowa DNR	LH Mid-grass	Harrison
Loess Hills SF-south	100	Iowa DNR	LH Mid-grass	Harrison
Murray Hill Overlook	10	CCB	LH Mid-grass	Harrison
Crossman Prairie	10	Iowa TNC	NE Mesic TG	Howard
Hayden Prairie	240	Iowa DNR	NE Mesic TG	Howard
Banwart Prairie	10	CCB	?	Humboldt
Pioneer Prairie Pothole	10	CCB	?	Humboldt
Ozark WA	10	CCB	Dry-mesic Lime TG	Jackson
Kish-Ke-Kosh Prairie	15	CCB	Dry-mesic TG	Jasper
Round Prairie Park	10	CCB	Mesic TG	Jefferson
Williams Prairie	20	Iowa TNC	Wet TG	Johnson
Smith Prairie	10	CCB	?	Kossuth
Stinson Prairie	30	CCB	NW Wet-mesic TG	Kossuth

Table 2. Continued.

Name	Estimated Acreage of Prairie	Management CCB = County DNR = State NPS = National Park Service TNC = The Nature Conservancy INHF = IA Natural Heritage Foundation	Primary and Secondary Prairie Communities HP = Hill Prairie LH = Loess Hills Lime = Limestone NE = Northeast NW = Northwest TG = Tallgrass	County
Denning Conservation Area	10	CCB	?	Lee
Hitaga Sand Ridge	20	CCB	?	Linn
Rock Island Botanical Preserve	10	CCB	Dry-mesic Sand TG	Linn
Gitchie Manitou Preserve	20	Iowa DNR	NW Mid-grass	Lyon
Maskunky Marsh	10	CCB	Wet Prairie	Mahaska
Rose Hill Marsh	10	CCB	?	Mahaska
Marietta Sand Prairie	15	CCB	Dry-mesic Sand TG	Marshall
Loess Hills WA	500	Iowa DNR	LH Mid-grass	Monona
Preparation Canyon SP	50	Iowa DNR	LH Mid-grass	Monona
Sylvan Runkel Preserve	300	Iowa DNR	LH Mid-grass	Monona
Turin Loess Hills Preserve	200	Iowa DNR	LH Mid-grass	Monona
Shield Prairie	20	CCB	?	Muscatine
Swamp White Oak Savanna	20	Iowa TNC	Oak Sand Savanna	Muscatine
McCormack Area	10	CCB	?	O'Brien
Ocheyedan Mound	10	CCB	NW Dry Tallgrass	Osceola
Burns Prairie	150	CCB	Wet-mesic TG	Palo Alto
Huston Prairie	50	CCB	?	Palo Alto
Larson Prairie	30	CCB	?	Palo Alto
Prairie Gold WA	80	CCB	?	Palo Alto
Road's End	10	CCB	?	Palo Alto
Telford Prairie	150	CCB	?	Palo Alto
Broken Kettle	2000	Iowa TNC	LH Mid-grass	Plymouth
Five Ridge Prairie	300	CCB	LH Mid-grass	Plymouth
Mt. Talbot Preserve	90	Iowa DNR	LH Mid-grass	Plymouth
O'Brien Prairie	30	CCB	?	Plymouth
Fonda Prairie	10	?	?	Pocahontas
Kalsow Prairie	120	Iowa DNR	Mesic TG	Pocahontas
Engledinger Marsh	10	CCB	Dry-mesic TG	Polk
Sand Hill	10	CCB	Mesic TG	Polk
Yellow Banks Park	10	CCB	Oak Savanna	Polk
Hitchcock Nature Area	50	CCB	LH Mid-grass	Pottawattamie
Vincent Prairie	20	INHF	LH Dry-mesic TG	Pottawattamie
Ringgold WA	20	Iowa DNR	?	Ringgold
Dinesen Prairie	20	CCB	Mesic TG	Shelby
Doolittle Prairie	25	CCB	Wet-mesic TG	Story
Pohl Prairie	10	Iowa TNC	Mesic TG	Story
Prairie Rail Trail	10	CCB	Mesic TG	Story
Medora Prairie	30	Iowa TNC	Mesic TG	Warren
Rolling Thunder Prairie	60	CCB	Mesic TG	Warren
Liska-Stanek Prairie	20	CCB	Mesic TG	Webster
Rosow Prairie	30	CCB	?	Webster
Chipera Prairie	20	CCB	?	Winneshiiek
Sioux City Prairie	150	CCB	LH Dry-mesic TG	Woodbury
Stone SP	20	Iowa DNR	LH Mid-grass	Woodbury
Panicum Prairie	10	CCB	?	Worth
Turkeyfoot Prairie	10	CCB	?	Worth
Worth County Lake	10	CCB	Wet-mesic TG	Worth
Prairie Smoke WA East	10	CCB	?	Wright
Prairie Smoke WA West	15	CCB	?	Wright

blooming populations of wood lily, prairie smoke, or fringed loosestrife. Northern species like oval-leaved milkweed can be found on a few remnants on the Iowan Surface. Northern limestone prairies occur on valley slopes where erosion has exposed the bedrock. Plant species to see on the limestone prairies include white camas and heart-leaved meadow parsnip. Further east on the Paleozoic Plateau, the hill prairies overlooking the Mississippi River are steeper and higher versions of the limestone prairies. Bird's foot violet and prairie coreopsis are fairly common on these rugged prairies.

The Mississippi Alluvial Plain boasts one of the largest and best-developed sand prairies at the Big Sand Mound, just south of Muscatine. Big Sand Mound is an active sand dune formed from wind-blown sand deposited on the alluvial plain. Species like hairy puccoon, eastern prickly pear, and goat's rue are easily found. Other sand prairies occur on the northeastern end of the Southern Iowa Drift Plain, for example at Marietta Sand Prairie along the Iowa River and at the Rock Island Botanical Preserve and Cedar Hills Sand Prairie, both along the Cedar River. Expect to see plants like blunt-leaved milkweed, showy tick trefoil, and flowering spurge at these sand prairies.

Southern versions of the limestone prairie also occur in the northeastern end of the Southern Iowa Drift Plain. These occur on older bedrock (of Silurian vintage) than the northern limestone prairies, which are mostly on Devonian limestones. A couple of species to see here are cylindrical blazingstar (which is also common on hill prairies) and Great Plains ladies-tresses.

High-quality savanna remnants are hard to find. Because they are so fire-dependent, they are probably the most endangered community on the prairie landscape. A few good places to get a feel for them on the Southern Iowa Drift Plain are at Rochester Cemetery, just east of Iowa City; at one of TNC's newest projects—a floodplain savanna called Swamp White Oak Preserve south of Iowa City; and at a thin soil, oak savanna currently under restoration at Yellow Banks County Park near Des Moines. A few of the characteristic plants found among these sites include shooting stars, early buttercup, cardinal flower, and purple milkweed.

Most of the Southern Iowa Drift Plain was draped with rolling mesic prairie, nicely exemplified by Sheeder Prairie and Bundt Prairie in Guthrie County. These are good places to see common species like tall cinquefoil, southern species like scaly blazingstar, or infrequent species like green milkweed. There are a couple of good examples of floodplain prairie on the Southern Iowa Drift Plain. One is William's Prairie along the Iowa River in eastern Iowa—home to bunchflower and marsh marigold. Another is a privately-owned site adjacent to the Nishnabotna River in southwestern Iowa. A naturally rare prairie community that I suspect occurred only sporadically on the Southern Iowa Drift Plain is sandstone prairie. An example occurs on Cretaceous deposits near Springbrook State Park.

A must-see for anyone's tour of Iowa prairie is the Loess Hills—the only place in Iowa that comes close to fulfilling a description of native rangeland. The original Hills must have been incredibly diverse, with a moisture gradient ranging from wet-mesic on the adjacent Missouri River floodplain to some of the driest environments in the state on the tops of southwest slopes, all occurring within a distance of less than a half-mile. Conspicuous plant species include yucca (the hallmark plant of the Hills), large flowered penstemon, pasque flower, and silky aster. The dry mid-grass prairies support several state endangered plants, for example, narrow leaved milkweed, cowboy's delight, and biscuit root.

One of the best remnants to visit on the Northwest Iowa Plains is Steele Prairie, a combination of mesic and wet-mesic prairie. Typical prairie species to see here are compass plant and cream false indigo. For a taste of the Great Plains, visit Gitche Manitou State Preserve in the extreme northwest corner of Iowa. Portions of the

preserve lie on Sioux Quartzite outcrops about 1.6 billion years old. It's the only place in Iowa with metamorphic bedrock at the surface. It's a tough, dry environment and a good home for species like fragile prickly pear cactus, golden aster, and fameflower.

WHAT LIES AHEAD?

Iowa's prairie remnants represent less than 0.1% of the original prairie landscape. It boggles my mind to imagine the prairie we could have today if only our forefathers had possessed the foresight to set aside a section or even a township of prairie here and there. Because that never happened, the only way we will ever see a whole tallgrass prairie ecosystem in Iowa is through restoration. It just might be possible. There are many, many people involved with reconstruction and restoration in Iowa. It's truly an exciting time because it is happening at many different levels—by federal, state, and county governments, and by conservation groups or corporations, by schools and businesses, and most impressively by many private individuals. Rebuilding the prairie landscape is a formidable task, certainly more difficult to do than was destroying it. It will take a lot of cooperation, and in Iowa I think we have a tremendous start.

There's Neal Smith National Wildlife Refuge, an 8,000 acre (3,200 ha) prairie and savanna restoration on the Southern Iowa Drift Plain east of Des Moines. Neal Smith offers our best hope at seeing a functioning tallgrass prairie ecosystem complete with growing herds of bison and elk. One of the most important characteristics of the prairie was simply its vast size. Neal Smith will at least solve that problem.

The Iowa Department of Transportation (DOT) and the Integrated Roadside Vegetation Management Program are making huge strides in the establishment of native prairie along the approximately 600,000 acres (242,800 ha) of roadsides in Iowa. The philosophy is simple, the best way to prevent weeds and control erosion along roadsides is to establish native vegetation. Nothing fills the soil with root mass better than a prairie. A fine example of one of the DOT's reconstructions is along Interstate 35 in Story County on the east side of Ames. Close to 130 species were used in the seeding, and about 85% of these are now established.

The Iowa DNR has been doing reconstructions for many years on its wildlife management areas, but perhaps one of the agency's more significant contributions has been the program to reintroduce the greater prairie chicken to southern Iowa grasslands. You can learn more about how the program is succeeding from Melvin Moe in his presentation on Wednesday morning.

One of the most amazing contributions to rebuilding the prairie landscape is coming from private landowners. I wish I knew for sure how many individuals are involved in these restoration projects. There must be many dozen at least, and they are spread out all over the state. This kind of grass roots approach is critically important if we are to have any chance of saving all the slivers strewn across the landscape.

This year, the Iowa Prairie Network (IPN) celebrates 10 years of educating the public about Iowa's prairie heritage. I'm positive that one reason there is such strong grassroots support for prairie is because of IPN's work in all seven regions across the state. A main IPN goal has been to get people out to see the prairies in their area by sponsoring field trips. Another has been to organize workshops that teach the public about prairie issues. There's no doubt it's working. For example, the central region of the IPN helped to sponsor a workday on a prairie remnant in Story County that was rapidly being lost to cedars. Over 75 people came out to help cut and carry cedars off the prairie. The result has been a dramatic recovery of a fine remnant that has populations of an uncommon species, Hill's thistle, and a federally listed species, slender bush clover. We need more of

this deep-rooted enthusiasm. Thanks to the Volunteer Conservation Corps (VCC) in the Council Bluffs area, there is no shortage of opportunities to show enthusiasm and help with these projects. The VCC is making sure that prairie workdays are occurring frequently in the southern Loess Hills.

The result of all of these efforts is that little by little we will continue seeing more and more healthy prairie. Still, if we expect to succeed, we need always to practice our foresight. What lies ahead? For one thing, certainly more of the same enthusiasm I've just described can be expected. But what are some of the problems or concerns that we should contemplate? Here are ten issues to work on:

The first is that we must do a good job planning and implementing the reconstructions. The use of seed sources that represent local ecotypes (i.e., populations within a species adapted to local environments) is certainly an important concern. An issue that remains largely unanswered, though, is what distance constitutes "local." Even more importantly, we need to make sure we are paying attention to the larger scale pattern of species biogeography. Despite all the expert planning and work that went into the Story County I-35 reconstruction (the Iowa DOT project described earlier), there are at least nine species that were planted that should not have been. One is ash sunflower, a southern tallgrass species that does not make it into central Iowa. Another is common wormwood, a species non-native to the U.S., and a third is decurrent false aster, a federally listed species with a natural range limited to floodplain habitats in southern Illinois and eastern Missouri.

Second—Despite all the good work being done, there is still a tremendous amount of prairie that can be saved if someone can just get to it in time. Nowhere is this more apparent than in the Loess Hills and on the northeast Iowa hill prairies, where nearly all the land is privately-owned and prairie continues to fade away under the greenery of invading cedars. But elsewhere in the state the same is true. Even near my home in Story County there is a remnant that I often drive by, and every year I see more trees and less prairie. And then there are the hidden pasture prairies in southern Iowa. It's not unusual to walk out into the back of someone's abandoned pasture and see a field of pale purple coneflowers. It's good that we have so many remnants to work with but unfortunate that it seems we don't have enough people-power or time to do the work. Most remnants are on private land and they need our help.

Third—We need to work harder to find and protect savannas, many of which are now more accurately described as pasture or cool-season savannas. They too are fading fast under the shade of encroaching trees. But they are out there, usually with a very degraded herb layer and a still recognizable canopy. The first step must be stopping the woody encroachment and restoring the canopy to a correct density of trees; then work can begin on restoring the herb layer. Unlike a tallgrass prairie, reconstruction of savanna with its oak component would take over a hundred years. The fact that these degraded savannas still have their canopy species intact makes rehabilitation much more efficient than reconstruction. We must not write the savanna remnants off.

Fourth—Railroad and cemetery remnants are often among the more common small prairies that have survived, and although some are well managed there are still many that are neglected. An organization like the Iowa Prairie Network needs to establish a dialogue with the railroad companies to educate their people and work towards some agreement on how best to manage railroad remnants. The Network can also foster grassroots action at the local level to provide education and support to Township trustees who oversee small rural cemeteries.

Fifth—More research and effort should be directed at management of exotic species like sweet clover, leafy spurge, Canada thistle, buckthorn, bird's-foot trefoil, and reed canary grass. We've got to be

vigilant in management and know how to treat at the first sign of encroachment. Nowadays, no remnant is completely safe from these pests.

Sixth—Managers must know and understand how fire affects prairies and use it carefully. I think most managers in Iowa do a pretty good job of subdividing remnants to protect invertebrate diversity. That's a must in good quality remnants. In situations where exotic plants are a major problem, fire needs to be used more aggressively, for example, later in the spring (like mid-May) or perhaps in the late summer and during periods of drought. We could do a better job of using fire to recreate the prairie environment and make it harsh enough to separate the true prairie species from the exotics. Overall, the most important concern regarding the use of prescribed fire is to be knowledgeable enough to express an explicit reason for using the fire in the first place.

Seventh—We need to get the remnants protected before suburban developers get to them. People generally don't build their dream homes out in a middle of a cornfield; they want a pretty spot with a view. That makes the less-suitable agriculture land, the very sites most likely to have remnants, more desirable building locations for these trophy homes. Pasture savannas seem to be especially attractive to developers.

Eighth—More research is needed on prairie insects, which undoubtedly comprise a huge component of the biodiversity on a prairie. What are their life cycle and life history patterns? How do they survive fires? How do they affect plant growth, pollination, and community structure? How are they important in the food chain? There are many questions and not enough answers.

Ninth—We should strive to change the federal requirements of the Natural Resource Conservation Service and Farm Service Agency to plant trees on land enrolled as riparian buffers in the Conservation Reserve Program (CRP). In some cases, these marginal riparian lands are prairie pasture remnants, in which case, tree planting is not the ideal management technique to conserve the native biodiversity. Furthermore, it's time we had a prairie conservation reserve program similar to the successful federal wetland reserve program and the state forest reserve program. There is no reason why owners of upland prairies should not receive the same type of incentive for choosing conservation as do owners of wetlands and forests. There is no conceivable reason, in this day of overproduction of farm crops, for remnant prairies to continue to be plowed up for more agricultural production.

Tenth—The questions and strategies relevant to prairies and the scenario of global warming need to be identified and addressed. Iowa's tallgrass climate lies in the area of overlap between the climates of grasslands and temperate forest. In other words, much of Iowa lies in an area that could be greatly affected by subtle changes in climate. What those changes will be during continued global warming remains to be seen. We do know that over the last century the Iowa climate cooled slightly (by 0.2°F) and precipitation increased by 20%. These are not trends that favor prairie. A big question is: to what extent should we battle a wetter climate with management techniques in order to maintain prairie? If we're lucky, maybe global warming will make our climate hot and dry and the whole state will naturally revert to prairie.

These are difficult and important issues to ponder. Maybe some of the answers will come out of the conference this week. I hope so. I'd sure hate to lose opportunities to see the soft evening light spread over and highlight the texture and color of a mid-summer prairie or the sunset on the silhouette of a lone savanna oak. One of the hardest tasks I had in putting this talk together was deciding which slides to leave out. There is much more wonderful prairie out there for you to see during your visit to Iowa. I hope all of you have a chance to

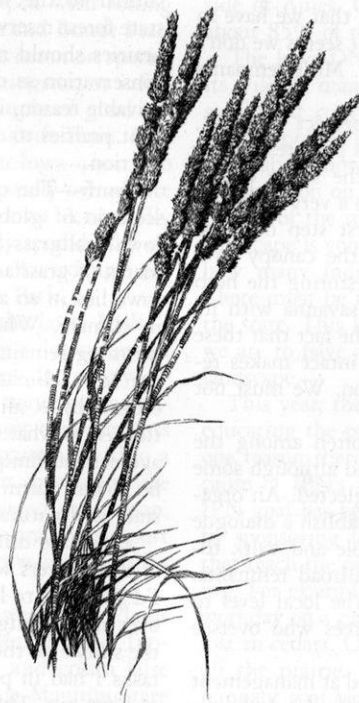
see and feel some of it up close. Have a great conference, a safe trip home, and come back soon.

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America's Lost Landscape: The Tallgrass Prairie

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The story of America's tallgrass prairie is rich and complex. At the time of Euro-American settlement, the 100 million ha tallgrass prairie was a major feature in mid-continent North America. In less than a century, most of the tallgrass prairie was converted to cropland. Nine states and provinces have lost more than 99% of their historic tallgrass prairie. This drastic alteration of the landscape contributed to the removal of the cultural imprint of the native populations who were more attuned to the prairie. A film, *America's Lost Landscape: The Tallgrass Prairie* is being produced by the author and David O'Shields to tell the story of the tallgrass prairie. The goal of this film is to inform and enlighten the general public and students about the historical, cultural and environmental aspects of the tallgrass prairie landscape and to address questions about the future of tallgrass prairie in an agriculturally dominated landscape. In this paper, aspects of making the film are interwoven with the story of the tallgrass prairie. Discussion topics include: the floral and faunal components, the original prairie landscape, the interaction of Native American and Euro-American cultures with the prairie, the basis for cultural perspectives and how these perspectives changed, individuals and events that are critical to the tallgrass prairie story, prairie settlement and the conversion of the prairie, development of a land ethic, the current perspective of the prairie, prairie restoration and challenges regarding the future of the tallgrass prairie.

INDEX DESCRIPTORS: tallgrass prairie, prairie landscape, film production, cultural perspective, cultural interaction, prairie settlement, Native American, Euro-American, agriculture, land ethic, sustainable agriculture, society, conservation.

I stood on a bluff east of the Little Sioux River; across the river, early morning mist drifted slowly over the glacial relicts of Cayler Prairie, one of the last major remnants of tallgrass prairie in Iowa. I had journeyed here before sunup to reflect and contemplate last things. In 1870, the last two bison in Iowa were sighted nearby at a fork of the Little Sioux, one year later, the last elk herd in the state was eliminated in this vicinity. Cayler Prairie was the site of the last state record for the Dakota skipper in 1992. Across the river, mist shrouded the prairie, the tops of knobs and eskers hung suspended above unseen kettles. Behind me, a few rays of the rising sun began to pierce the clouds, highlighting an ethereal land. Before me, my mind's eye surveyed a surreal scene of refracted images, blurred relicts of the past, ghostly reflections, and diminishing reality. Normality was arrested as time and place were transcended; I felt the chill of a stray zephyr wafting off ice gone more than ten millennia. In the unnatural stillness, the faint sound of shivering grass drifted down from past centuries carrying the indistinct thuds of hooves of departing bison and the faint haunting bugle of a spirit elk. The tallgrass prairie was a swirling kaleidoscope of incomplete visions, limited consciousness, historical vignettes and ancestral memory. I was peering through a window in time. The prairie of the past was just beyond my grasp, and I yearned to take wing and soar across the river to merge with it.

My revelry was interrupted by the sharp slam of a hog feeder and the ignition of a tractor motor. These abrupt intrusions were reminders that I live in an agriculturally dominated landscape. However, I cherish that fleeting moment when I saw through time. That brief time warp encapsulated something I have pursued for more than a quarter of a century.

Like John Madson (1972), my feelings are akin to those of "a modern man who has fallen in love with a face in a faded tintype. Only the frame is still real, the rest is illusion and dream. So it is with original prairie. The beautiful face of it had faded before I was born, before I had a chance to touch and feel it, and all that I have

known of the prairie is the setting and the mood—a broad sky of pure and intense light, with a sort of loftiness to the days, and the young prairie born winds running past us from open horizons."

For 28 years, I have been attempting to know and understand the elusive tallgrass prairie. I have walked and crawled on prairies, laid out transects and sampled quadrats on prairies, burned prairies, observed, studied and read about prairies, planted and transplanted prairie species, helped preserve prairies and cried over destroyed prairies. I have attempted to recreate tallgrass prairie on college campuses, school grounds, cornfields, roadsides, and in my mind. I have tried to tell and retell the story of the tallgrass prairie so that I and others could better understand it. In the process, I have become increasingly convinced we need the prairie because it is part of our past. Much of the biological inheritance of the "naked ape" of Desmond Morris (1967) was developed in the forests of Africa, but our cultural inheritance is tied to experiences on the intervening grasslands as our ancestors climbed down from the trees, stood erect, developed stereo vision and expanded their mind.

The story of the tallgrass prairie, its inhabitants and their interrelationships is important. For more than a quarter of a century, I was frustrated by the lack of a film that truly depicted the tallgrass prairie. I finally decided to attempt to tell the story of this lost landscape. To accomplish that task, I teamed with film director David O'Shields of New Light Media to produce the film, *America's Lost Landscape: The Tallgrass Prairie*. The goal of this film is to inform and enlighten the general public and students about the historical, cultural and environmental aspects of the tallgrass prairie landscape, and to address questions about the future of tallgrass prairie in an agriculturally dominated landscape. This paper is an attempt to convey the content, topics and issues of the subject matter and discuss the challenges and experiences involved in capturing the images needed to visually tell the story.

The tallgrass prairie was immense, encompassing a triangular area west from the Wabash River across the Missouri River into the east-

ern Dakotas, Nebraska and Kansas. The southwest corner of Wisconsin, almost all of Iowa, southwestern Minnesota and northwestern Missouri formed the core. From this core, it extended south across east-central Oklahoma into Texas and north into Manitoba. All in all, it was a 100 million ha swath of tallgrasses that stretched down out of southern Manitoba, broadened to 965 km through the Midwest, and extended more than a 1600 km to the Gulf of Mexico.

What is now the state of Iowa occupied the heart of the tallgrass prairie. Tallgrass prairie dominated Iowa and was an integral part of more than 80% of the landscape, 11.33 million ha in all (Smith 1998). The northern half of the state, except for the northeast corner, had been modified, directly or indirectly, by the last glacier creating an extensive swell and swale prairie and prairie pothole wetlands. The southern part of the state, except for the eastern edge along the Mississippi, had not been glaciated for 500,000 to 2,500,000 yrs. This older, more dissected landscape was dominated by a mixture of oak savanna and tallgrass prairie (Prior 1991).

In filming the tallgrass prairie, it is essential to capture a sense of its vastness so the viewer can appreciate the extent of the original prairie. John Madson (1982) says that to really be prairie it has to reach to the horizons. In Iowa, you have to cheat a bit and shoot uphill into the sky to capture that feeling. To obtain images of the vastness of the tallgrass prairie we had to travel to South Dakota, the Nebraska Sandhills, the Flint Hills of Kansas and the Osage Hills of Oklahoma. Although open space is important, there are other aspects of prairie. Smaller remnants scattered among the crop-fields provided beautiful close up illustrations of plants and animals and their interrelationships.

A good quality prairie contains more than 250 different plant species, each individual plant occupying vertical and horizontal niches both above and below ground for maximum utilization of the space. These plants are both beautiful and utilitarian, and, for me, invoke feelings of awe and wonderment as well as continuity with the past. Nothing is more relaxing than lying on your back on a late summer day and viewing the deep blue sky through the out stretched turkey feet of big bluestem. What can compare to the carpeted beauty of rod after rod of blazing star reaching to the horizon. Words can't express the feelings that form as one views the rare, white-fringed prairie orchid. The brilliant oranges of the Turk's cap and prairie lilies are extremely photogenic. The uniqueness of the flowers and fruit of prairie smoke, rattlesnake master and Indian plantain account for at least part of their beauty. The delicate beauty of the exploding floral arrangement of an individual shooting star is equal only to the awesome visual impact in late May of hundreds upon hundreds of them forming a white to lavender in green patchwork quilt. A late September day is brightened by the colorful contrast of the giant blue lobelia, purple gentian, or New England aster against the curing grasses. One has to admire the tenacity of pale purple coneflowers that have reestablished in a roadside or railroad right-of-way as an annual proclamation of once existing prairie. The "prairie birthday" essay by Aldo Leopold (1949) has established the compass plant as a symbol of the vanishing prairie.

The entire film could consist of shot after shot of the large variety of prairie plants. The challenge is to provide a sufficient variety of grass and wildflower shots to illustrate the astonishing beauty of the individual species and the ever changing panorama of the growing season without visually saturating the audience. Furthermore, the floral display has to be balanced with a depiction of the more elusive animals that interact with the plants to form the dynamic biotic community. The prairie biota, both above and below ground components, is an essential aspect of the tallgrass story.

The extensive root systems and other components of underground prairie are often overlooked even though they are an integral part of tallgrass prairie. It is estimated that the underground portion of

prairie plants exceeds 65% of the total vegetative biomass of the plants. The root systems of different species stratify vertically and develop more extensively at specific levels. This reduces competition for water and nutrients and provides for maximum utilization of the underground space. The extensive root systems enable the prairie plants to survive the stress of extremes of heat and cold as well as limited moisture. Unlike trees and shrubs, grasses and forbs die back to the ground during winter. Shielded by their blanket of soil and sod, the roots and buds for next year's growth lie dormant and safe from desiccating winds and winter temperatures as low as -40°C at ground level (Bailey and Anderson 1980). This same feature enables the prairie plants to withstand prairie fire and flourish afterward. In a fire, above ground temperatures may reach 200°C while two to five cm below ground the temperature rises less than 2°C (Bailey and Anderson 1980). In addition, these extensive root systems are largely responsible for the formation of the fertile black soils that underlie the tallgrass prairie region.

The extensive underground prairie is difficult to capture on film. In the past, researchers have excavated large 3–5 m deep trenches to expose the root systems. With the limited amount of prairie remaining, we did not consider that to be an option. Current researchers are using special cameras to record underground activities and minimize disturbance. Valuable information about the interactions of the root systems and associated soil flora and fauna can be derived from these indirect observations.

Fire was an integral part of the prairie landscape, but opinions vary as to whether it was a primary cause in the development of prairie or a factor in maintaining the prairie. As prairies became more extensive, it is likely that fire became more prevalent. Dry lightning storms in summer could ignite fires which could cause extensive burns of continuous grasslands on gentle to rolling terrain when winds and temperatures were high and humidities low. Later, the early American big game hunters increased the frequency of prairie fires and extended the burn season to spring and fall (Anderson 1990).

Fire benefits the prairie by increasing plant diversity, stimulating growth and flowering of individual plants, killing or stunting woody invaders, converting litter to usable nutrients, creating darkened soil that warms quickly in the spring and favors warm-season prairie species over cool season invaders, and delaying or preventing aging of certain prairie plants. Without fire, a prairie will become degraded and overrun with brush (Henderson 1982).

Preventing fires favors forest over prairie. If a tallgrass prairie is not burned for two decades, it will be heavily invaded by woody species and no longer resemble a prairie. Shrubs are the initial woody invaders with gray dogwood and smooth sumac being the most aggressive. These early shrub invaders modify the environment permitting the establishment of trees. These shrubs are often stimulated by spring burns, but they can be curtailed by burns during other seasons.

As indicated, fire is such an integral part of the tallgrass prairie that no film of this ecosystem would be complete without it. We were able to film a number of small prescribed burns, but to fully illustrate the magnitude of fire on the original prairie landscape, we wanted to obtain visuals of a large fire that stretched to the horizon. Some of the large scale prescribed burns on Konza Prairie fit that criterion. However, fire weather doesn't always adhere to filming schedules, two fire seasons were required to obtain the desired footage. During the first season, we had a film and sound crew on standby for 3 days (a rather expensive undertaking), but the winds were either too strong or from the wrong direction for the prescribed burn, and we couldn't film. Finally in late March of 2000, we were able to shoot a 400 ha burn on Konza Prairie. The filming of that prescribed burn was one of the high points of the entire project. The

Konza burn crew ignited the fire about 1445 and completed the task about 2100 after sunset. The bright flames against the night landscape and the reflections of fire off the billowing smoke provided a spectacular finale.

Native Americans and the Prairie

While a nature film of the prairie would be satisfying to some, the full story of the tallgrass prairie is more than that. The interactions of the prairie and people who inhabited it are very important. The cultures of the people who came to live on the prairie influenced their perspective of the prairie. Conversely, the prairie affected the people, and they responded by modifying their cultures.

Humans first moved onto the tallgrass prairie as the last glaciers were retreating to the north. These early prairie occupants were probably descendants of the nomads who came down from the Arctic although other possible origins have been suggested. For thousands of years, these people lived primarily by hunting and moving about in small bands. They traveled light, with animal skins for protection against the elements and weapons and tools made of stone and bone for killing and processing game. They developed a culture adapted to their natural environment. As a hunting and gathering society, these early small groups of Native Americans had a limited impact on the tallgrass prairie. According to the classic viewpoint, they did not exhaust or extinguish resources and left them in a usable state for succeeding generations. Living in close contact with the land, they saw themselves as a part of the natural community, one of many species in a complex system on the landscape. They were an integral part of the land where they lived and possessed a "sense of place." In spite of being well-adapted to their environment, their lives were somewhat uncertain as they were largely at the mercy of weather as well as the waxing and waning of game and food plants. They felt a need for assistance from a host of spirits that inhabited the natural world. According to their religious beliefs, the earth was alive and nature was a divine order that was to be respected and disturbed as little as possible. Plants and animals were seen as brotherly manifestations of the Great Spirit; killing them was done carefully, apologetically and ritualistically to meet the basic needs of survival (Krech 1999). The tribes who relied more on agriculture than hunting did little to disturb the tallgrass prairie as they farmed on the margins and were few in number.

In the film, we attempt to convey a realistic picture of the interaction of Native American cultures with the tallgrass prairie. This was no easy task as opinions differ regarding the relationship of Native American cultures to the environment. To many, they lived in harmony with the land, and were, to paraphrase Wes Jackson (1994), native to this place. However, from our modern perspective, we must avoid romanticizing the relationship of Native Americans with the land and bestowing on them conservation motives that they did not possess. It must be kept in mind that they were relatively few in number and hadn't developed the necessary tools and technology to over-exploit the land. Nevertheless, they had much less impact on the tallgrass prairie than the Euro-American settlers.

Advertising campaigns have reinforced a long-held assumption that Native Americans were the first ecologists (Nash 1990). However, bison driven off cliffs in numbers exceeding food needs, excessive localized disturbances, depleted land and forests as well as disappearance of entire populations due to possible over exploitation of limited resources, suggest that Native Americans were not always careful stewards of Mother Earth. Consequently, scholars continue to debate the extent to which they were, in fact, ecologists. The best explanation is that they were not ecologists in the sense of the environmentalists of the 20th century. On the other hand, most of their religions emphasized the need to kill with "reverence" so as

not to upset the powerful spirits that inhabited the universe of two-legged and four-legged creatures. In contrast to the biblical book of Genesis, in which God creates man in his own image and gives him dominion over all other creatures, the Native American legends reflect the view that human beings are no more important than any other, whether alive or inanimate. In the eye of the Creator, they believe, man and woman, plant and animal, water and stone, are all equal, and they share the earth as partners—even as family (Kopper 1986, Krech 1999).

Native American use of fire is an important feature of the story of the tallgrass prairie. These early Americans found fire to be an effective tool. To create islands of fresh grass and attract herbivores, they used fire to remove dead plant material and stimulate plant growth in the early spring. Fire was also used to control animal movement while hunting, to clear areas around campsites, and to remove trees along streams to create garden plots. Accidental fires were started when signaling or leaving cooking fires burning in abandoned camps. Early explorers often encountered burned areas or areas being burned by natives. Frontier artists such as Catlin, Miller, Ranney, Tait and Deas commonly depicted fire in their paintings. The use of fire by Native Americans was so extensive that it apparently altered the landscape. It is generally assumed that their burning expanded and maintained the eastern portion of the tallgrass prairie and checked the spread of the forest vegetation (Anderson 1990, Pyne 1982).

Euro-Americans and the Prairie

How people interact with nature and the land is primarily determined by the culture of their society. In the film, we illustrate how the societies perceived the prairie to help audiences understand and appreciate the interaction of cultures with the prairie. A comparison of the Native American and Euro-American cultures is inevitable as there were definite differences in their attitudes toward nature and the land. The Euro-Americans clearly have been the more exploitative of the two cultures. It is difficult to discern whether this was due to inherent cultural differences, differences in numbers of people or differences in technological tools.

The European immigrants came to North America from a society that had much earlier made the transition from hunting/gathering to agriculture. In the transition, their culture changed as their society began to lose contact with nature. Later, a renaissance in science and technology created an industrialized society that was even more removed from nature. The separation from nature increased early in the 17th century with the acceptance of Francis Bacon's opinion that it was necessary for society to conquer and subdue nature and wrench her secrets from her. To squelch "nature worship" in those formative times, science and the church allied to create a dichotomy of "knowledge as good" and "nature as evil" (Keller 1985). As a result, European immigrants arrived in the new world with the belief that nature was hostile, evil and chaotic. Unfortunately, their experiences often confirmed their worst fears. Therefore, from their first arrival, they behaved as though nature must be either subdued or ignored. In New England, the Puritans drew on scriptural passages to support the drive to subjugate nature and to labor for profit. Their cultural perspective was fused with the belief that they were a special people and that people who differed from them were "aliens."

While the European immigrants were establishing themselves in America and becoming Euro-Americans, John Locke was developing a new definition of land value. According to his thesis, the value of land was derived from the labor done on it and the benefits that resulted from this labor. The right of use and ownership was determined by the farmer's labor. As a corollary, Locke considered wilderness or uncultivated land synonymous with waste (Hargrove

1988). Locke's philosophy appealed to the Euro-American settlers and was easily incorporated into their culture.

Thomas Jefferson was attracted to Locke's ideas and envisioned the yeoman farmer as the backbone of a republic stretching from the Atlantic to the Pacific. Early in the 19th century, President Jefferson dispatched Lewis and Clark to investigate the newly-acquired Louisiana Territory with the hope of opening a new land west of the Mississippi. The westward moving settlers who followed in the wake of Lewis and Clark carried the banner of Manifest Destiny with them. They felt it was ordained that this was to be their land from sea to shining sea (Billington 1960).

Evidence of how well Locke's philosophy was incorporated into the culture of the Euro-Americans was illustrated in 1858 at the 25th "old settlers" reunion in Burlington, Iowa. Speaker after speaker reflected on the accomplishments of the past quarter century of settlement and boasted of making the wasteland around them productive (Antrobus 1915). Modern land use decisions often reflect the persistence of this cultural perspective.

Clash of Cultures and Settlement of the Tallgrass Prairie

As the North American continent was settled, there were numerous clashes of Native American and Euro-American cultures. As noted in the film, *Black Hawk*, a Sauk war chief, was a pivotal person in the settlement of the tallgrass prairie. In part, he is representative of the many Native Americans who unsuccessfully resisted the westward push of the Euro-Americans, but more important, his actions resulted in the Black Hawk War and the subsequent Black Hawk Treaty of 1832, which opened the tallgrass prairie for settlement. The archives of the Iowa and Wisconsin historical societies provided excellent images depicting this period.

For a time after the turn of the 19th century, Euro-American settlement of the tallgrass prairie was halted at the Mississippi River. The prairie of northwest Indiana and northern Illinois was settled, but the ancestral Ioway territory west of the river belonged by treaty to the Sioux, Sauk and Fox. This fragile line of demarcation began to crumble with Black Hawk's ill-advised decision to cross the Mississippi River into Illinois to return to his ancestral village near the mouth of the Rock River. When the Sauk band crossed the river, fear of an Indian attack spread throughout the Euro-American settlements of Illinois. An army of regular soldiers and volunteers was quickly formed to meet the perceived threat. Black Hawk refused an order to move to the Iowa side of the Mississippi River and retreated north in the hope of gaining support from allies. For 15 weeks, the army pursued Black Hawk and his supporters across Illinois and Wisconsin. They were finally trapped against the Mississippi River and crushed in a battle near the mouth of the Bad Axe River in southwest Wisconsin. Approximately 150 Sauk men, women, and children were ruthlessly massacred. To save the lives of the rest of his people, Black Hawk surrendered to the United States government and signed the Black Hawk Treaty of 1832. The treaty opened part of Iowa for settlement and was the first of several Indian cessions that cleared the way for the Euro-American settlement of the tallgrass prairie (Sage 1974). The brutal treatment of Black Hawk's band in the battle at the Bad Axe River may have discouraged Indian resistance to future cessions of land. The response to the opening of the tallgrass prairie for settlement was swift as settlers from adjoining areas and distant locations poured into the Iowa Territory and beyond. Within the next 70 years almost all of the tallgrass prairie was settled.

The Euro-Americans who settled the tallgrass prairie did not co-exist with the land, they waged a war with it. To provide for their families, they had to subdue the prairie and convert it to cropland. They were fighting for survival in a hostile environment that could

easily overwhelm any civilized gain. Initial motivation to make the wasteland productive was provided by cultural forces. Later, society provided the technology needed to accelerate the conversion of prairie to cropland and justified the conversion with a self-ordained mandate to feed the world. As a consequence, the tallgrass prairie was plowed and planted into oblivion in less than a century.

Edwards (1948) conjectured that the westward moving pioneers had an impression of everlasting immensity when they first viewed the tallgrass prairie in northwest Indiana and northeast Illinois, "... the pioneers hesitated on the edge of the large prairies with their seemingly endless expanse of thick grass. There was a sense of vastness about them that seemed overpowering, an impression of greatness that could not be subdued." However, the Western culture of the Euro-Americans prevailed. They considered the tallgrass prairie a place to be conquered or a vessel to be improved by making it productive. They proceeded to carve farmsteads out of the prairies and savannas. Their endeavors were accelerated by a technological revolution which continually expanded the mechanization of agriculture. Tallgrass prairie was converted to cropland at an incredible rate. As an area was settled, the prairie and the prairie animals were eliminated in less than a decade. According to Dinsmore (1994), the mean interval between the first permanent settlement in a county and the last record of a bison was six years.

The rich, black soil created by the extensive roots and rhizomes of the underground tallgrass prairie provided the foundation for an extensive agricultural economy. The soil of the tallgrass prairie of Iowa, northern Illinois, southwest Minnesota, northwest Missouri is exceedingly productive, accounting for almost all of the high-quality agriculture land in the United States. Iowa, alone, contains 25% of all the Grade A land in the contiguous 48 states (Marbut 1934). The development of this fertile prairie land provided for the emergence of the United States as a world leader in agriculture.

In *The Unsettling of America*, Wendell Berry (1977) wrote that "we came with vision, but not with sight. We came with visions of former places, but not the sight to see where we are." In retrospect, the magnitude and rate of the loss of the tallgrass prairie is unbelievable. It seems that once the Euro-Americans acquired the technological equipment needed to convert prairie to cropland they couldn't stop until it was gone. Leopold (1949) pessimistically observed, "Man always kills the things he loves, and so we the pioneers have killed our wilderness. Some say we had to. Be that as it may, I am glad I shall never be young without wild country to be young in." John Madson (1972) eloquently summarized the process, "We spent our tallgrass prairie with a prodigal hand and it probably had to be that way, for these are the richest farm soils in the world. There were certain wilderness things that were fated to be spent almost to the vanishing point: bison in the shortgrass plains, lobos and grizzlies in the settled cattle country—and the vistas of true prairie."

Most of the original tall grass prairie landscape has vanished. Nine states and provinces have lost more than 99% of their historic prairie. Fragments of the remaining prairie remnants are widely scattered across their former range—isolated islands awash in an agricultural sea. The blacksoil prairies were the hardest hit; Manitoba, North Dakota, Illinois, Indiana, Wisconsin, Illinois and Iowa lost more than 99.9% of their original prairie while Minnesota and Missouri lost 99.6% and 99.5% respectively. The greatest quantity of prairie was lost in Iowa with 11.33 million ha reduced to less than 11,330 ha.

An analogy of a "prairie puzzle" may be helpful for developing an understanding of the loss of 99.9% of an ecosystem. For example, if the original Iowa prairie were a 1000 piece puzzle, only one piece of the entire puzzle would remain. Furthermore, that single piece would be fragmented into hundreds of smaller pieces. To continue the analogy, the scattered remnants have been degraded so the frag-

mented pieces would be damaged. Perhaps a dog chewed the fragments or they went through the wash in a jeans pocket.

A Land Ethic

By the middle of the 20th century, the Euro-American view that land must be conquered and made productive had resulted in a greatly diminished, fragmented tallgrass prairie ecosystem. If there was any hope for this rapidly vanishing landscape, society needed a different cultural perspective.

Two generations after the tallgrass prairie was considered settled, Aldo Leopold proposed a "Land Ethic" as an alternative to human subjugation of the land. According to Leopold (1949), "The land ethic simply enlarges the boundaries of the community to include soils, waters, plants, and animals, or collectively: the land . . . In short, a land ethic changes the role of *Homo sapiens* from conqueror of the land-community to plain member and citizen of it. It implies respect for his fellow-members, and also respect for the community as such."

The film portrays Aldo Leopold as another pivotal person in the story of the tallgrass prairie. His "Land Ethic" (1949) provided a new paradigm for the reassessment of our relationship to the natural world. To comprehend this view of land as a community, and man as a too often, unaware member of it, Leopold suggested that we look upon history not as a story of human enterprise alone, but as a complex tale of interaction of humanity's ambition and techniques with the land's natural diversity and dynamism.

The film interviews of the Leopold children, Nina and Carl, and the filming of the Leopold shack stirred memories and emotions. The writings of "Sand County Almanac" came alive. We discovered that the shack is more than a symbol for conservation and the environmental movement. Both Nina and Carl were adamant that the shack and the family experiences associated with it were cherished by the Leopold family.

Current Perspective of the Prairie

Prairie remnants are preserved as examples of our biological heritage and no longer have to be productive to be of value. The legacy of Leopold and others who labored to increase awareness of the value of natural systems has borne fruit. Interest in prairie has steadily increased in the past 40–50 years. Hundreds of prairie enthusiasts have been meeting biennially since 1968 to discuss prairie preservation, restoration, management, research, interpretation, flora and fauna. Groups interested in prairie have formed across the Midwest to share prairie experiences and to promote prairie. It is unfortunate that the prairie ecosystem had to decline almost to the vanishing point before there was an awareness of what was being lost.

Private organizations such as The Nature Conservancy and governmental agencies continue prairie preservation activities while implementing programs to restore the tallgrass prairie. Large scale tallgrass prairie ecosystem preservation and restoration projects are well underway at Konza Prairie in the Flint Hills of Kansas, the Tallgrass Prairie Preserve in Osage County, Oklahoma, and the Niobrara Valley Refuge in the Nebraska Sandhills. Large scale attempts are underway to restore or reconstruct tallgrass prairie and savanna ecosystems on agricultural land at the Neal Smith (Walnut Creek) National Wildlife Refuge and Prairie Learning Center near Prairie City, Iowa and at the Midewin Tallgrass Prairie and the Fermi Laboratory Prairie in northern Illinois. In addition, many local prairie enthusiasts and land owners are personally reconstructing or restoring native prairie.

The concept of using native vegetation in roadsides to control weeds and beautify the landscape is gaining acceptance across the United States and in many other parts of the Western World. Be-

cause prairie is the native vegetation in mid-continent North America, it is logical for the Integrated Roadside Vegetation Management (IRVM) Programs of Iowa, Minnesota and surrounding states to utilize native prairie in roadsides to control weeds and woody species. Roadsides for prairie establishment are an extensive resource. In Iowa alone, there are 243,000 ha of roadsides, most of which were, and could be again, prairie. States within the tallgrass prairie region could unite to form an extensive multi-state roadside prairie network.

It was heartening that so many foundations, governmental agencies, private organizations, companies and individuals were willing to support the telling of the story of *America's Lost Landscape: The Tallgrass Prairie* by contributing almost one-half million dollars to the production of the film. This reflects a change in our society's cultural perception of tallgrass prairie.

Tallgrass Prairie of the Future

Part of the film involved conjuring up nostalgic memories of the tallgrass prairie of the past, a relatively easy task. However, ascertaining the tallgrass prairie of the future presented a real challenge. Will it have a place in the modern agriculture and urban landscape, will it be completely obliterated and memorialized only in names of towns, streets and developments, or will our society learn from the past and include tallgrass prairie in our future? Is it possible to recover the tallgrass prairie? Much depends upon how tallgrass prairie is valued in our culture. Wes Jackson (1994) asserts that we must "become native to this place, to base our culture and agriculture on nature's principles." This has become increasingly more difficult as so much cultural information has been lost and continues to be lost.

To a large extent, the future of the tallgrass prairie and agriculture are intertwined. When considering the question regarding the prairie of the future, it might be well to review conditions of our agriculturally-dominated landscape. There is: (1) a need for sustainability, (2) a high use of energy and chemicals in crop production, (3) a loss of 25 billion tons of topsoil annually, (4) flooding and siltation of streams, (5) an ever increasing "dead zone" in the Gulf of Mexico, (6) a loss of natural beauty, and (7) a decline in spirit. Our society emphasizes production, profit and economic growth over all else. We focus on product at the expense of process. In a sense, we have unknowingly robbed ourselves of our natural environment and heritage. It has been suggested that our society exists within a natural world of oozing wounds. Is it our destiny that the tallgrass prairie ecosystem will slowly expire from these wounds on our watch?

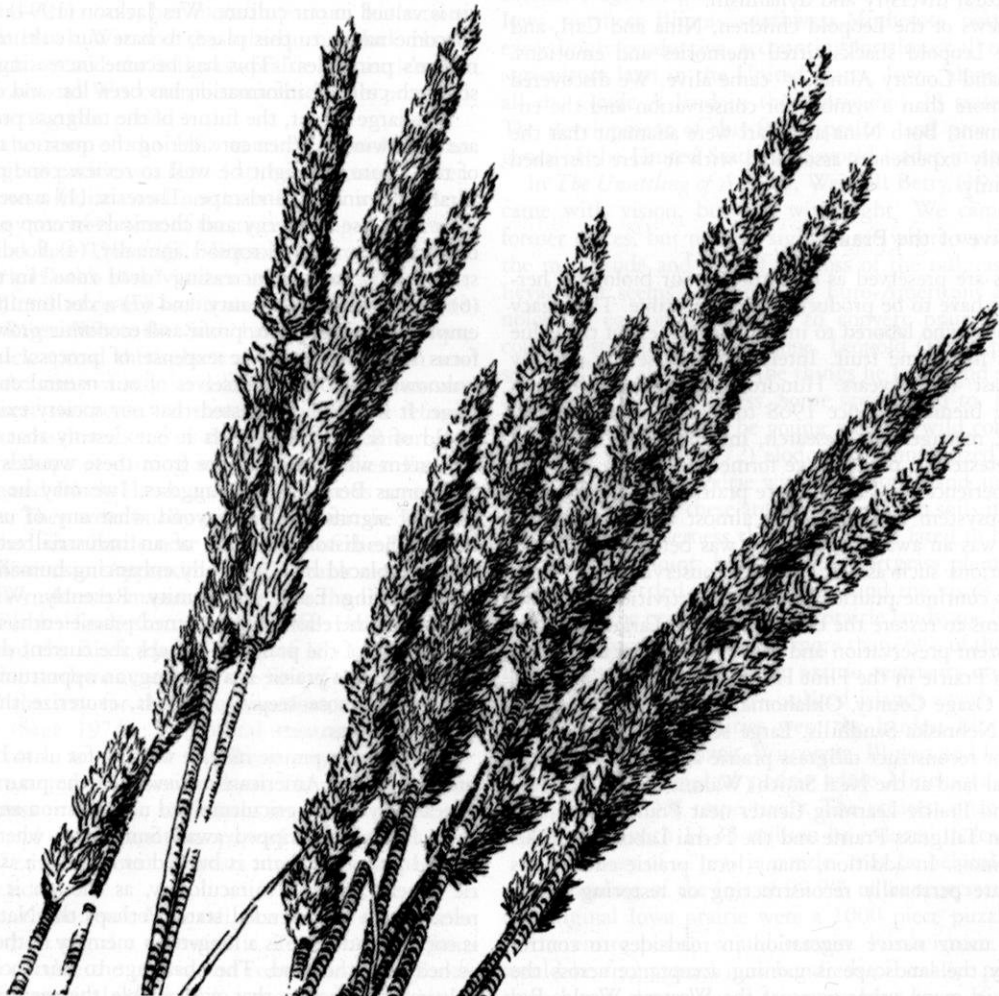
Thomas Berry (1999) suggests, "we may be experiencing a moment of significance far beyond what any of us can imagine." He thinks the distorted dream of an industrial technological paradise can be replaced by a mutually enhancing human presence within an ever-renewing Earth community. Recently, William Witt (1999) chronicled the efforts of concerned prairie enthusiasts who are aiding the "return of the prairie." Perhaps the current diminished condition of the tallgrass prairie is a blessing, an opportunity to come together to staunch those seeping wounds, cauterize them, and begin the healing process.

The tallgrass prairie may be waiting for us to begin the restoration process. Native Americans believe that the prairie continues to exist beneath layers of agriculture and urbanization and will emerge when these layers are stripped away. Sometimes when an apparently degraded prairie remnant is burned or cleared, a striking, diverse prairie appears, almost miraculously, as though it had been awaiting release from a suspended state. Perhaps the Native American belief is correct, and there is a long-term memory of the prairie community etched into the land. The challenge to our society is to nurture a cultural perspective that will enable the reemergence and reestab-

ishment of the tallgrass prairie ecosystem. The future of humanity may well hang in the balance.

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Floristic Comparisons of Tallgrass Prairie Remnants Managed by Different Land Stewardships in Eastern South Dakota

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Over the last 150 years the tallgrass prairie ecosystem has been almost completely decimated on a continental scale. Although South Dakota retains a relatively large amount (~15%) of original sod of this diverse plant and animal community, sodbusting is still occurring, and much of what remains of tallgrass prairie is intensively grazed or otherwise poorly managed. The Wilhelm Floristic Assessment Method was used to evaluate the floristic quality of 63 tallgrass prairie remnants managed under different land use regimes and stewardships (private, public and reference) in eastern South Dakota. Grazing was the dominant land use on 26 of 31 privately owned tracts; publicly managed tracts (n = 29) were 96% idle; and reference tracts (n = 3) were managed with prescribed fires. A total of 277 plant species were detected on the 63 sites with average species richness values of 82 for private, 79 for public, and 119 for reference tracts. Forty-four (16%) of the 277 species were exotics. Only two species, smooth brome grass and Kentucky bluegrass, were found on all 63 sites. Mean C values (\bar{C} , where C = Coefficient of Conservatism) and Floristic Quality Index (FQI) values averaged higher on reference tracts (average \bar{C} = 5.7, mean FQI = 57) than on public (average \bar{C} = 5.3, mean FQI = 44) or private tracts (average \bar{C} = 4.9, mean FQI = 39) indicating that tallgrass prairie varies in quality depending on land management practices.

INDEX DESCRIPTORS: floristic quality, assessment, tallgrass prairie remnants, reference areas.

Tallgrass prairie is one of the most endangered ecosystems in the United States (Samson and Knopf 1996). Dominated by big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*) and switchgrass (*Panicum virgatum*), tallgrass prairie once comprised an estimated 575,000 km² of land in the central United States (Knapp and Seastedt 1986). Spanning from southern Canada to Texas and from eastern South Dakota and Nebraska eastward to Illinois and parts of Indiana (Küchler 1964), the tallgrass prairie was once one of the most extensive vegetation types in North America. Many ecologists agree that less than one percent of the tallgrass prairie remains in the United States today (Knapp and Seastedt 1986, Keystone Center 1991, Samson and Knopf 1994).

States in the eastern part of the tallgrass prairie have experienced the greatest loss of this ecosystem. About 0.01% or less of native tallgrass prairie remains in Indiana, Illinois, Wisconsin, North Dakota, Iowa, and Manitoba; Minnesota retains about 0.04% of its original prairie (Samson and Knopf 1996). States retaining larger portions of native tallgrass prairie include Texas (10%), South Dakota (15%), and Kansas (18%) (Samson and Knopf 1996).

Prairie remnants of various sizes are scattered throughout the range of tallgrass prairie. The highly fragmented nature of this landscape isolates prairie patches within a dominant agricultural matrix and poses a myriad of problems (i.e., edge effect, reduced habitat size, etc.) for the natural ecosystem (Forman 1997). Organisms concentrated in these remnants become increasingly susceptible to extirpation as patch size shrinks and land management intensifies (MacArthur and Wilson 1967). Genetic depression, climatic change, dispersion, and competition with exotic plants are some of the most pressing issues facing species found on insular tracts of tallgrass prairie

(Rabinowitz and Rapp 1980, Keystone Center 1991, Poiani and Johnson 1991, Guertin et al. 1997).

Management practices on the remnant tallgrass tracts can stress species found there and ultimately reduce biological diversity. Both overuse and neglect from a management perspective can adversely influence tallgrass prairie biota. The consequences and implications of land managers' practices are being scrutinized in regard to possible effects on biological diversity and sustainability.

Divergent attitudes of rangeland ecologists and conservation biologists about the effects and appropriateness of grazing have resulted in divergent land use practices on tallgrass prairie remnants (West 1993, Fleischner 1994, Noss 1994). Grazing of livestock on some areas may alter floristic composition and wildlife use (Duebber and Kantrud 1974, Damhoureyeh and Hartnett 1997). Selective grazing by introduced herbivores, mainly cattle, often favors grasses over forbs and woody vegetation (Damhoureyeh and Hartnett 1997). Wildlife that prefer low vegetation stature excel on tracts of intensively grazed prairie (Clark and Kaufman 1991); whereas species adapted to greater amounts of cover are disadvantaged (Kirsch et al. 1978, Fleischner 1994).

Idle lands also are receiving increased attention because of concern about loss of biodiversity due to congested vegetation cover (Rice and Parenti 1978, Knapp and Seastedt 1986). Tracts of tallgrass prairie remaining idle for extended periods of time accumulate excessive amounts of litter which can reduce light availability, alter moisture capacities, and decrease accessibility to seedbeds (Rice and Parenti 1978, Knapp and Seastedt 1986). Consequences of litter build-up include reduced competition of native versus introduced plant species and inability of native species to become established due to lack of suitable substrate (Rice and Parenti 1978). Although

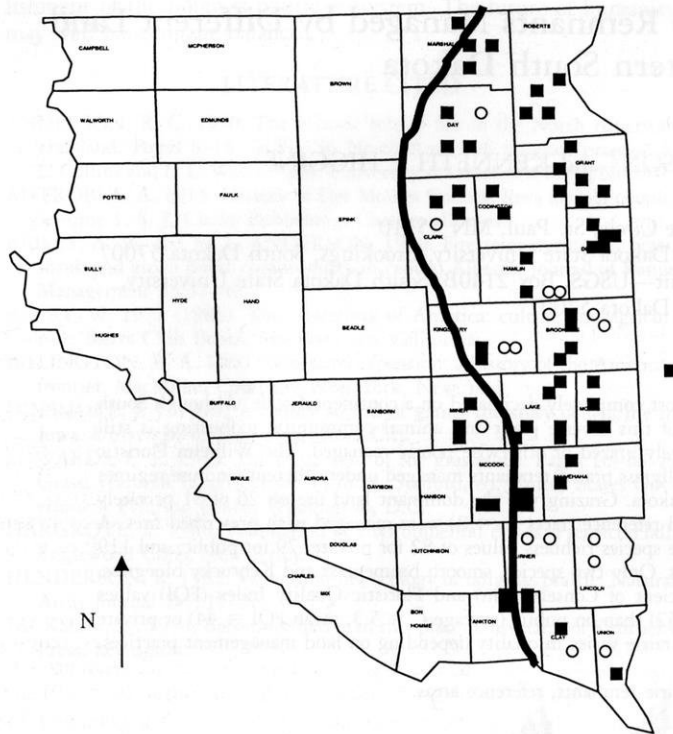


Fig. 1. Tallgrass prairie study site distribution in the 20 eastern-most counties of South Dakota, 1998. Each symbol represents one study area ($n = 79$). Black boxes approximate location of evaluated sites ($n = 63$), circles represent sites not evaluated ($n = 16$). The symbol east of the South Dakota boundary represents the Pipestone National Monument site in Pipestone, MN. Dark line roughly represents the historic western boundary of tallgrass prairie in South Dakota (adapted from Küchler 1964).

some wildlife species prefer deep litter, others prefer a mosaic of litter depths scattered throughout an area (Kirsch et al. 1973, Clark and Kaufman 1991).

Another threat to biodiversity in tallgrass prairie is invasion by exotic plants, especially noxious weeds. According to Westbrooks (1998), weed invasion is second only to habitat destruction as a threat to native biodiversity. Several noxious weeds threaten the tallgrass prairie ecosystem, including leafy spurge (*Euphorbia esula*), plumeless thistle (*Carduus acanthoides*), perennial sow-thistle (*Sonchus arvensis*), and Canada thistle (*Cirsium arvense*). Other introduced species, such as smooth brome (*Bromus inermis*) and Kentucky bluegrass (*Poa pratensis*), while not classified as noxious weeds, are nonetheless problematic to maintaining native plant diversity in tallgrass prairie.

The tallgrass prairie association (*Andropogon-Panicum-Sorghastrum*) is home to hundreds of plant and animal species, but much of this wildlife habitat has been decimated by the transformation of natural land cover to agricultural cropland. Recent interest at a national level to inventory and evaluate the condition of native ecosystems has focused attention on the tallgrass prairie and its various components. The goal of this project was to provide baseline data on the floristic integrity of native tallgrass prairie remnants as influenced by management practices in eastern South Dakota.

STUDY AREAS

According to Küchler (1964), tallgrass prairie is potentially supported in the 20 easternmost counties of South Dakota (Fig. 1). As

tallgrass prairie remnants exist today, they can be broadly grouped into three ownership categories: privately owned, publicly owned, and privately owned/managed preserves (the latter mostly owned and managed by The Nature Conservancy). Most remaining tallgrass prairie occurs on private lands with lesser amounts in public ownership or private preserves. Although management varies with ownership and among tracts, some land-use generalizations are apparent. Privately owned tracts are largely used for livestock grazing, primarily cattle, sheep, and horses, and they are managed with a variety of grazing systems. Most are continuously grazed during the growing season. Public lands (owned by federal and state agencies) are primarily managed for wildlife production. Management practices on public lands vary from some inclusion of fire and grazing to remaining idle. Native prairie preserves are managed largely to preserve or rehabilitate the native ecosystem to approximate pre-settlement conditions (Clint Miller, pers. comm.). We refer to the private preserves as reference areas in this study.

METHODS

Selection of Study Sites

Originally, the study sites selected for this project were to be ≥ 16 ha, with half of the sites on publicly owned lands and half on privately owned lands. An additional goal was to have three private and three public study sites located within each of the 20 easternmost counties in South Dakota. The limited availability and small sizes of native prairie parcels, however, often dictated smaller and unevenly distributed sites. For example, because of flooding in northern counties and the low number of native tracts ≥ 16 ha in general, a few study sites were as small as two ha.

Potential study sites on public lands (federal and state) were identified from maps maintained at Federal Wetland Management District offices and at South Dakota Game, Fish and Parks offices in each county. Three public study sites per county were selected randomly when the possible choices exceeded three; however, several counties did not have enough publicly owned prairie remnants to produce three paired sites. Thirty-eight sites on public lands were initially selected (Fig. 1) for this study.

Thirty-eight privately owned remnants were then selected using aerial photographs maintained by the Farm Services Agency (FSA) offices in each county. Tracts labeled as "Y" or "NC" (both non-cropped) on aerial photos were assumed to meet selection criteria. Ownership of tracts was determined through public records, and owners were contacted in order to obtain access.

Private and public sites were paired based on proximity to each other in an effort to reduce variable environmental effects (e.g., soils and local climate). Most paired sites were within 10 km of each other and within the same county, however, paired sites were sometimes in different counties.

Three reference areas were selected from among several prairie preserves in the region. None of the reference areas had a tillage history and all were perceived to represent the best preserved examples of upland tallgrass prairie in our region. One of the reference areas is on the Pipestone National Monument in southwestern Minnesota; the other two, Sioux Prairie and Crystal Springs Preserve, are owned and managed by The Nature Conservancy and are located in Moody and Deuel counties, South Dakota, respectively.

Sixteen (20%) of the 79 pre-selected study sites were ultimately rejected (Fig. 1) due to conversion to agriculture, submergence by nearby wetlands, or evidence of past cultivation. Of the disqualified sites, seven were privately owned and nine were publicly owned. None of the pre-selected study sites in Turner and Lincoln counties qualified for this study and were therefore excluded. Results of this study were thus based on the remaining 63 study sites. Land use on

privately owned study sites ($n = 31$) was predominantly grazing ($n = 26$; 84%) but with several ($n = 5$; 16%) idle at least up to the time of survey. All but one of the publicly owned sites ($n = 29$) were idle when evaluated. All of the reference sites ($n = 3$) were idle when evaluated, and part or all of each area had been burned during 1998. Some of the private and public sites had been partially burned earlier in the growing season or the preceding fall.

Floristic Assessment

Each study site was evaluated using the Wilhelm Floristic Assessment Method (Swink and Wilhelm 1994). Others have used this method, or modifications of it, in various areas of the Midwest (Taft et al. 1996, Ladd 1997, Masters 1997, Packard and Ross 1997). Floristic assessment was developed to provide a consistent and efficient means of evaluating the floristic quality of natural areas. An *a priori* value called the Coefficient of Conservatism, or C-value, was assigned to each native species in a region. C-values ranged from 0 to 10 based on a species' ability to indicate or predict site quality. Species indicative of high quality undisturbed tracts were assigned higher values, while species poor at indicating prairie quality received lower values (Appendix 1).

For example, prairie larkspur (*Delphinium virescens*) is only found in prairies that lack a tillage history and are not intensively grazed. The C-value assigned to prairie larkspur was thus 10. Plant species occurring on native prairies but also in areas with a disturbance history were assigned more moderate values. Big bluestem (5), heath aster (*Aster ericoides*) (4), and skeleton plant (*Lygodesmia juncea*) (5) are all examples of plants found on disturbed as well as high quality sites. Some taxa, such as cocklebur (*Xanthium strumarium*) may be native components of the ecosystem, but they tend to occur in disturbed habitats that may or may not be part of a native prairie. Often considered undesirable weeds, these species are not indicators of site integrity. Thus, cocklebur and similarly behaving species were assigned a C-value of 0 in the South Dakota tallgrass prairie region. Exotic species such as smooth brome grass were not assigned C-values because they did not evolve within this ecosystem and it would be inappropriate to judge site quality based on their presence (Appendix 2).

The C-value assigned to a particular species is generally applicable only on a regional basis, because ecotypic variation and other factors can affect a species' ability to indicate site condition from region to region. Therefore, different C-values often need to be assigned to a species in different regions. We collaborated with David Ode (state botanist, S.D. Game, Fish and Parks) and Eric Fairlee (graduate student/biological technician, South Dakota State University) to assign C-values to the tallgrass prairie species encountered in this study (Appendix 1).

The C-values from a complete species inventory are averaged to calculate the mean C (\bar{C}) for a particular tract of land. In addition, a Floristic Quality Index (FQI) can be calculated with the formula:

$$FQI = \bar{C}\sqrt{N},$$

where \bar{C} is the mean C for a site, and N is the total number of native plant species found on the site. The FQI is a more valuable index than \bar{C} alone because it incorporates native species richness into an estimate of quality.

A walking floristic inventory was conducted once at each study site during July or August, 1998, by a team of two or three people. Wetland areas were avoided so that many facultative or obligate wetland species (Reed 1988) were omitted from the checklist. Each study site was surveyed until no new species had been encountered in 30 minutes of walking. Unknown plants were collected, pressed, dried, and subsequently identified at the C. A. Taylor Herbarium,

Table 1. Summary of species richness on tallgrass prairie remnant study sites in eastern South Dakota, 1998.

	No. Sites	Mean No. of Spp.	SE	Range	% Exotics
Private	31	82	±5.9	28–132	18
Public	29	79	±7.8	21–132	14
Reference	3	119	±12.6	95–137	13

South Dakota State University. Nomenclature follows *The Flora of the Great Plains* (Great Plains Flora Association 1986) except for some instances where nomenclature has recently changed.

Statistical comparisons of \bar{C} and FQI values between land ownership categories were conducted using PROC MIXED (SAS Institute Inc. 1997). The F test was used to determine if differences existed among land ownership categories. Least square means were calculated and used to test for differences between any two ownership categories, and differences were considered significant at $P \leq 0.05$.

RESULTS

Species richness varied considerably among sample sites, ranging from 21–137 species, but averaging much higher on reference sites ($\bar{x} = 119$) than on either private ($\bar{x} = 82$) or public ($\bar{x} = 79$) sites (Table 1). Native flora represented 45 families, 125 genera, and 231 species (Appendix 1). Eight major tallgrass prairie indicator species occurred on the 63 remnant prairie sites with the following frequencies (number of sites in parentheses): big bluestem (59), little bluestem (52), Indiangrass (38), switchgrass (44), side-oats grama (53), leadplant (51), purple prairie clover (50), and Maximilian's sunflower (35).

Exotic species represented 13 families, 36 genera, and 46 species (Appendix 2); they comprised 18, 14, and 13% of private, public, and reference sites, respectively (Table 1). The only two species found on every study site were the exotics, smooth brome grass (*Bromus inermis*) and Kentucky bluegrass (*Poa pratensis*). In combination, native and exotic species comprised 47 families, 156 genera, and 277 species. Of this total, grasses, forbs, and shrubs were represented by 57, 217, and 3 species, respectively.

Mean Coefficient of Conservatism (\bar{C}) across all site categories ranged from 2.0–6.0. The \bar{C} for private lands was significantly lower ($P = 0.02$) than for public lands (Table 2). The \bar{C} for public and private site categories did not differ significantly ($P = 0.09$) from that of reference sites possibly due to the low sample size of reference sites ($n = 3$) (Table 2). The floristic quality of study sites measured by the FQI showed a range from 12 to 63 (Table 2). There was no statistical difference between the FQI values on public (44) and private (39) sites ($P = 0.19$) nor between public and reference sites ($P = 0.10$) (Table 2). The mean FQI for privately owned study sites (39) was significantly lower ($P = 0.03$) than for reference sites (57).

DISCUSSION

The results of this study demonstrate that many remaining tallgrass prairie relicts in South Dakota are depauperate of plant species compared to our reference sites. Extreme fragmentation of the natural landscape in the tallgrass prairie region of South Dakota, combined with intensive use (usually season-long grazing) on most remaining tracts is undoubtedly decreasing plant diversity. This is reflected in the comparatively low species richness values obtained on both private and public tracts.

Only those species found predominantly in upland habitats were

Table 2. Summary of floristic quality assessment values (mean C and floristic quality index) for private, public, and reference tallgrass prairie study sites in eastern South Dakota, 1998.

Ownership	No. Sites	Mean C			FQI		
		Mean*	SE	Range	Mean*	SE	Range
Private [a]	31	4.9 ^a	±0.14	2.9–5.9	39 ^a	±2.4	12–63
Public [b]	29	5.3 ^b	±0.14	2.0–5.9	44 ^{ab}	±2.5	11–62
Reference [c]	3	5.7 ^{ab}	±0.44	5.3–6.0	57 ^b	±7.7	55–62

*Means with the same letter superscripts are not significantly different ($P < 0.05$) from each other

included in the inventory, therefore the number of species is less than some other published lists (Howe 1994, Knapp et al. 1998). In addition, the one-time survey method used to inventory the tracts may have forfeited some detail in lieu of expediency; however, all study sites were inventoried in the same manner. Also, heavy grazing on some of the tracts may have contributed to fewer plant species being detected than were actually present on those sites.

Despite invasion by exotic species and various intensive management practices (i.e., season-long grazing, herbicide application, etc.) many remnant prairie tracts supported some species typical of high quality prairie (Appendix 1). This indicates that common tallgrass prairie species are at least somewhat resistant to exotic plant competition and adaptable to a variety of management regimes. However, native plant populations could be slowly succumbing to those same influences and could ultimately disappear as pressure continues.

Wilhelm Floristic Assessment

In order to establish a standardized method of efficiently (i.e., consistently, effectively, and relatively rapidly) evaluating prairie remnants, the Wilhelm Floristic Assessment Method was used to characterize the floristic quality of our study sites. Results from this evaluation were as predicted, with reference areas showing the highest site quality and public and private areas reflecting lower quality and diversity. The low number (3) of reference areas limited the strength of statistical analyses, but trends are readily apparent.

Statistical analyses showed that privately owned prairies have significantly lower \bar{C} values than public sites. Reference areas were not significantly different from either of the other categories, but this was undoubtedly attributable to the low sample size. Invasive exotic species, like smooth brome grass, tend to extirpate the more sensitive species first, i.e., those with higher C-values, thus reducing \bar{C} over time. Given a history of heavy grazing and various other types of disturbance, it is not surprising that privately owned tracts contained the highest percentage (18%) of exotic plant species. Publicly owned and reference study sites had lower percentages of introduced species, 14 and 13%, respectively.

Whereas \bar{C} summarizes the general floristic status, the Floristic Quality Index (FQI) is a better measure of the ecological integrity of a site. Privately owned lands averaged much lower FQI values than those of reference sites; however, publicly owned sites did not differ significantly from reference sites. Again, this is likely due to the low sample size for reference sites. Public and private lands did not differ significantly ($P \leq 0.05$) in FQI values.

According to Swink and Wilhelm (1994), areas with an FQI of 35 or less do not contain enough native species to be seriously considered for preservation efforts in the Chicago region. The privately owned tallgrass prairie tracts analyzed in this study yielded an average FQI of 39, indicating the floristic biodiversity of the tallgrass prairie ecosystem has suffered in eastern South Dakota. Season-long intensive grazing on some of these areas has altered the floristic com-

position through selective grazing, influenced competition for resources (e.g., light, moisture, nitrogen, etc.) and established or maintained populations of undesirable plants (exotic, often noxious species).

Swink and Wilhelm (1994) also suggested that areas with FQI values approaching 45 are good representatives of natural areas and should be considered for preservation. Publicly owned lands, which are presently conservation areas, averaged near this mark with a mean FQI of 44. This moderate FQI value may reflect some loss of diversity due to past management when these areas were privately owned (Kirsch et al. 1978), or may be partly attributable to current management practices. All except one of the publicly owned study sites were idle at the time of evaluation. As has been shown, long term idling of native prairie reduces or eliminates native species due to excessive litter accumulation and increased competition from exotic species that tend to excel under idle conditions (Leach and Givnish 1996, Knapp and Seastedt 1986).

On the other end of the spectrum are those areas of excellent floristic quality, with mean FQI values close to 60. As suspected, the tracts that represented the most diverse prairies in this study were the reference sites. Our three reference sites have all been subjected to a variety of management practices, most notably haying (at least historically) and/or periodic burning, but grazing on all three has been very limited in the past and is not permitted now. The remarkably high FQI values demonstrate that the consequences of management practices on these sites have been positive. Although there are only a few good quality preserves in eastern South Dakota, our reference sites illustrate that with proper management the potential exists to rehabilitate tallgrass prairie tracts in this region.

Based on our findings, we believe a majority of tallgrass prairie remnants in eastern South Dakota retain a complement of plant species that would enable some degree of rehabilitation, despite the presence of exotic invaders. We also believe that the Wilhelm method of vegetation evaluation has good potential for assessing the directional (positive or negative) effects of various grassland management treatments in eastern South Dakota and adjacent tallgrass prairie areas. A committee of plant taxonomists and prairie ecologists has recently developed standardized C-values for all native vascular plant species in the northern Great Plains region with emphasis on North and South Dakota (Northern Great Plains Floristic Quality Assessment Panel 2000). Another team of ecologists is finalizing an inventory of tallgrass prairie remnants based on Farm Service Agency map data (Higgins et al. 2000). A holistic approach using results from these projects should enable better preservation and management strategies for the remaining tallgrass prairie in the northern Great Plains.

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APPENDIX 1. Native vascular plant species detected during inventories of 63 remnant tallgrass prairie tracts in South Dakota, 1998, their assigned C-values and frequencies.

Family	Latin Name	Common Name	C-value ^{ab}	No. of Sites of Occurrence	Frequency %
Amaranthaceae	<i>Amaranthus albus</i>	Tumbleweed	0 (1)	1	2
	<i>Amaranthus retroflexus</i>	Redroot pigweed	0 (1)	9	14
Anacardiaceae	<i>Toxicodendron rydbergii</i>	Poison ivy	2 (2)	14	22
Apiaceae	<i>Zizia aptera</i>	Heart-leaf golden alexander	10 (10)	23	37
	<i>Zizia aurea</i>	Golden alexander	9 (7)	13	21
Apocynaceae	<i>Apocynum cannabinum</i>	Indian hemp	4 (4)	36	57
Asclepiadaceae	<i>Asclepias ovalifolia</i>	Oval-leaf milkweed	9 (10)	3	5
	<i>Asclepias speciosa</i>	Showy milkweed	4 (1)	3	5
	<i>Asclepias syriaca</i>	Common milkweed	0 (0)	27	43
	<i>Asclepias verticillata</i>	Whorled milkweed	3 (1)	47	75
	<i>Asclepias viridiflora</i>	Green milkweed	8 (10)	20	32
Asteraceae	<i>Achillea millefolium</i>	Common yarrow	3 (1)	53	84
	<i>Agoseris glauca</i>	False dandelion	8	9	14
	<i>Ambrosia artemisiifolia</i>	Annual ragweed	0 (0)	33	52
	<i>Ambrosia psilostachya</i>	Western ragweed	3 (1)	55	87
	<i>Ambrosia trifida</i>	Giant ragweed	0 (1)	2	3
	<i>Antennaria neglecta</i>	Pussytoes	5 (4)	24	38
	<i>Antennaria parvifolia</i>	Pussytoes	6	5	8
	<i>Artemisia biennis</i>	Biennial wormwood	0 (1)	36	57
	<i>Artemisia campestris</i>	Western sagewort	5 (5)	17	27
	<i>Artemisia dracunculus</i>	Silky wormwood	5 (1)	2	3
	<i>Artemisia frigida</i>	Fringed sage	4 (1)	31	49
	<i>Artemisia ludoviciana</i>	White sage	4 (1)	56	89
	<i>Aster ericoides</i>	Heath aster	4 (5)	57	91
	<i>Aster laevis</i>	Smooth blue aster	9 (9)	1	2
	<i>Aster oblongifolius</i>	Prairie aster	9 (10)	27	43
	<i>Aster sericeus</i>	Silky aster	9 (10)	32	51
	<i>Chrysopsis villosa</i>	Golden aster	5 (5)	15	24
	<i>Cirsium flodmanii</i>	Flodman's thistle	6	53	84
	<i>Cirsium undulatum</i>	Wavy-leaved thistle	6 (1)	6	10
	<i>Conyza canadensis</i>	Horseweed	0 (0)	22	35
	<i>Echinacea angustifolia</i>	Purple coneflower	6 (3)	47	75
	<i>Erigeron glabellus</i>		9	1	2
	<i>Erigeron philadelphicus</i>	Philadelphia fleabane	3 (4)	3	5
	<i>Erigeron strigosus</i>	Daisy fleabane	5 (5)	37	59
	<i>Euthamia graminifolia</i>	Viscid euthamia	5 (4)	4	6
	<i>Gaillardia aristata</i>	Blanket flower	7 (1)	3	5
	<i>Grindelia squarrosa</i>	Curly-cup gumweed	0 (1)	29	46
	<i>Haplopappus spinulosus</i>	Cutleaf ironplant	4	4	6
	<i>Helianthus annuus</i>	Common sunflower	0 (1)	6	10
	<i>Helianthus maximiliani</i>	Maximilian's sunflower	5 (1)	35	56
	<i>Helianthus nuttallii</i>	Nuttall's sunflower	8	6	10
	<i>Helianthus pauciflorus</i>	Stiff sunflower	8 (8)	39	62
	<i>Heliopsis helianthoides</i>	Ox-eye	5 (5)	27	43
	<i>Hieracium canadense</i>		6 (6)	2	3
	<i>Iva xanthifolia</i>	Marshelder	0 (1)	5	8
	<i>Kuhnia eupatorioides</i>	False boneset	4 (6)	40	63
	<i>Lactuca ludoviciana</i>	Prairie lettuce	7 (10)	34	54
	<i>Lactuca oblongifolia</i>	Blue lettuce	5	41	65
	<i>Lactuca serriola</i>	Prickly lettuce	0 (1)	7	11
	<i>Liatris aspera</i>	Rough gayfeather	8 (6)	35	56
	<i>Liatris ligulistylis</i>	Rocky Mountain gayfeather	10	1	2
	<i>Liatris punctata</i>	Dotted gayfeather	7 (1)	39	62
	<i>Lygodesmia juncea</i>	Skeleton plant	5	31	49
	<i>Prenanthes aspera</i>		8 (8)	5	8
	<i>Prenanthes racemosa</i>	Rattlesnake root	8 (8)	4	6
	<i>Ratibida columnifera</i>	Yellow prairie coneflower	4 (1)	52	83
	<i>Ratibida pinnata</i>	Gray prairie coneflower	4 (4)	1	2

APPENDIX 1. Continued.

Family	Latin Name	Common Name	C-value ^{ab}	No. of Sites of Occurrence	Frequency %
	<i>Rudbeckia hirta</i>	Black-eyed Susan	5 (1)	10	16
	<i>Rudbeckia laciniata</i>	Golden glow	6 (5)	1	2
	<i>Silphium laciniatum</i>	Compass plant	5 (5)	1	2
	<i>Solidago canadensis</i>	Canada goldenrod	1 (1)	52	83
	<i>Solidago gigantea</i>	Giant goldenrod	4 (4)	18	29
	<i>Solidago missouriensis</i>	Missouri goldenrod	4 (7)	47	75
	<i>Solidago mollis</i>	Soft goldenrod	5	36	57
	<i>Solidago nemoralis</i>	Gray goldenrod	4 (4)	29	46
	<i>Solidago ptarmicoides</i>	Sneezewort aster	8 (10)	10	16
	<i>Solidago rigida</i>	Stiff goldenrod	4 (4)	50	79
	<i>Xanthium strumarium</i>	Cocklebur	0 (1)	9	14
Boraginaceae	<i>Lithospermum canescens</i>	Hoary puccoon	8 (8)	45	71
	<i>Lithospermum incisum</i>	Fringed puccoon	8 (8)	25	40
	<i>Onosmodium molle</i>	False gromwell	9 (9)	50	79
Brassicaceae	<i>Arabis hirsuta</i>	Rock cress	6 (6)	17	27
	<i>Erysimum inconspicuum</i>	Small flower wallflower	7 (1)	22	35
	<i>Lepidium densiflorum</i>	Peppergrass	0 (1)	11	17
Cactaceae	<i>Opuntia fragilis</i>	Little prickly pear	5	1	2
Campanulaceae	<i>Lobelia spicata</i>	Spiked lobelia	6 (6)	12	19
Caprifoliaceae	<i>Symphoricarpos occidentalis</i>	Buckbrush	3 (2)	41	65
Caryophyllaceae	<i>Cerastium arvense</i>	Prairie chickweed	4 (6)	13	21
	<i>Silene antirrhina</i>	Sleepy catchfly	0 (1)	1	2
Commelinaceae	<i>Tradescantia bracteata</i>	Spiderwort	7 (1)	2	3
Convolvulaceae	<i>Calystegia macounii</i>	Hedge bindweed	4	3	5
	<i>Calystegia sepium</i>	Hedge bindweed	4 (1)	13	21
	<i>Convolvulus arvensis</i>	Field bindweed	0 (1)	39	62
Cyperaceae	<i>Carex brevior</i>	Fescue sedge	4 (4)	27	43
	<i>Carex grvida</i>	Heavy sedge	5 (4)	8	13
	<i>Carex ballii</i>	Hall's sedge	8	1	2
	<i>Carex inops</i>	Sun sedge	7 (5)	3	5
	<i>Carex lanuginosa</i>	Wooly sedge	5 (4)	2	3
	<i>Carex praegracilis</i>	Clustered field sedge	6 (1)	5	8
	<i>Carex tetanica</i>		9 (9)	1	2
	<i>Carex vulpinoidea</i>	Fox sedge	2 (2)	12	19
Equisetaceae	<i>Equisetum arvense</i>	Common horsetail	6 (0)	4	6
	<i>Equisetum laevigatum</i>	Smooth horsetail	5 (2)	34	54
Euphorbiaceae	<i>Euphorbia dentata</i>	Toothed spurge	0 (1)	3	5
	<i>Euphorbia maculata</i>	Spotted spurge	0 (0)	2	3
	<i>Euphorbia marginata</i>	Snow-on-the-mountain	0 (1)	2	3
	<i>Euphorbia nutans</i>	Eyebane	0 (0)	1	2
Fabaceae	<i>Amorpha canescens</i>	Lead plant	9 (9)	51	81
	<i>Astragalus adsurgens</i>	Standing milk-vetch	8	2	3
	<i>Astragalus agrestis</i>	Field vetch	7 (1)	7	11
	<i>Astragalus canadensis</i>	Canada milk-vetch	8 (10)	25	40
	<i>Astragalus crassicaarpus</i>	Buffalo bean, Groundplum	8 (1)	16	25
	<i>Astragalus flexuosus</i>	Pliant milk-vetch	6	25	40
	<i>Astragalus missouriensis</i>	Missouri milk-vetch	5	6	10
	<i>Dalea candida</i>	White prairie clover	9 (9)	32	51
	<i>Dalea purpurea</i>	Purple prairie clover	9 (9)	50	79
	<i>Desmodium canadense</i>	Canada tickclover	6 (4)	6	10
	<i>Glycyrrhiza lepidota</i>	Wild licorice	5 (1)	43	68
	<i>Lathyrus venosus</i>	Bushy vetchling	9 (9)	4	6
	<i>Lotus unifoliatus</i>	Deer vetch	2 (1)	18	29
	<i>Oxytropis lambertii</i>	Lambert's crazyweed	5	9	14
	<i>Psoralea argophylla</i>	Silver-leaf scurfpea	6 (1)	51	81
	<i>Psoralea esculenta</i>	Prairie turnip	8	31	49
	<i>Strophostyles leiosperma</i>	Slick-seed bean	6 (9)	2	3
	<i>Vicia americana</i>	American vetch	6 (7)	11	17

APPENDIX 1. Continued.

Family	Latin Name	Common Name	C-value ^{ab}	No. of Sites of Occurrence	Frequency %	
Gentianaceae	<i>Gentiana affinis</i>	Northern gentian	10	1	2	
	<i>Gentiana andrewsii</i>	Bottle gentian	10 (8)	9	14	
	<i>Gentiana puberula</i>	Downy gentian	10 (10)	3	5	
Iridaceae	<i>Sisyrinchium campestre</i>	Blue-eyed grass	10 (10)	12	19	
Lamiaceae	<i>Dracocephalum parviflorum</i>	Dragonhead	3 (1)	1	2	
	<i>Hedeoma hispidum</i>	Rough false pennyroyal	2 (2)	10	16	
	<i>Lycopus asper</i>	Rough bugleweed	4 (1)	23	37	
	<i>Mentha arvensis</i>	Mint	4 (5)	10	16	
	<i>Monarda fistulosa</i>	Wild bergamot	4 (4)	20	32	
	<i>Salvia reflexa</i>	Lance-leaved sage	0 (1)	1	2	
	<i>Scutellaria parvula</i>	Small skullcap	10 (10)	4	6	
	<i>Stachys palustris</i>	Hedgenettle	5 (5)	17	27	
	Liliaceae	<i>Allium stellatum</i>	Pink onion	8 (10)	41	65
		<i>Lilium philadelphicum</i>	Wood lily	10 (10)	5	8
<i>Smilacina stellata</i>		False Solomon's seal	5 (5)	8	13	
<i>Zigadenus elegans</i>		White deathcamas	8 (10)	12	19	
Linaceae	<i>Linum rigidum</i>	Wild flax	5	2	3	
	<i>Linum sulcatum</i>	Annual flax	7 (8)	26	41	
Malvaceae	<i>Sphaeralcea coccinea</i>	Scarlet globe mallow	5	1	2	
Nyctaginaceae	<i>Mirabilis hirsuta</i>	Hairy four o'clock	4 (1)	35	56	
	<i>Mirabilis nyctaginea</i>	Wild four o'clock	0 (1)	3	5	
Onagraceae	<i>Calylophus serrulatus</i>	Cutleaf evening primrose	7 (10)	35	56	
	<i>Gaura coccinea</i>	Scarlet gaura	6 (1)	35	56	
	<i>Oenothera strigosa</i>	Common evening primrose	0 (0)	26	41	
Orchidaceae	<i>Spiranthes magnicamporum</i>	Lady tresses	8 (8)	1	2	
Oxalidaceae	<i>Oxalis dillenii</i>	Gray wood sorrel	4 (1)	40	63	
	<i>Oxalis stricta</i>	Yellow wood sorrel	0 (1)	2	3	
	<i>Oxalis violacea</i>	Violet wood sorrel	7 (9)	2	3	
Plantaginaceae	<i>Plantago patagonica</i>	Patagonian plantain	3 (1)	1	2	
Poaceae	<i>Agrostis scabra</i>	Ticklegrass	2 (5)	16	25	
	<i>Andropogon gerardii</i>	Big bluestem	5 (5)	59	94	
	<i>Aristida purpurea</i>	Red threeawn	4 (5)	4	6	
	<i>Bouteloua curtipendula</i>	Side-oats grama	8 (8)	53	84	
	<i>Bouteloua gracilis</i>	Blue grama	7 (1)	38	60	
	<i>Bouteloua hirsuta</i>	Hairy grama	7 (8)	4	6	
	<i>Buchloe dactyloides</i>	Buffalograss	4 (1)	7	11	
	<i>Calamagrostis stricta</i>	Northern reedgrass	5 (5)	15	24	
	<i>Calamovilfa longifolia</i>	Prairie sandreed	5	32	51	
	<i>Dichanthelium leibergii</i>	Leiberg's dichanthelium	10 (10)	12	19	
	<i>Dichanthelium oligosanthes</i>	Scribner's dichanthelium	9 (9)	40	63	
	<i>Dichanthelium wilcoxianum</i>	Wilcox's dichanthelium	7 (10)	5	8	
	<i>Echinochloa muricata</i>	Barnyard grass	0 (0)	4	6	
	<i>Elymus canadensis</i>	Canada wildrye	4 (4)	34	54	
	<i>Elymus trachycaulus</i>	Bearded wheatgrass	7 (8)	37	59	
	<i>Eragrostis cilianensis</i>	Stinkgrass	0 (1)	2	3	
	<i>Koeleria macrantha</i>	Junegrass	7 (7)	36	57	
	<i>Muhlenbergia asperifolia</i>	Scratchgrass	2 (1)	8	13	
	<i>Muhlenbergia cuspidata</i>	Plains muhly	8 (10)	31	49	
	<i>Muhlenbergia richardsonis</i>	Mat muhly	8	1	2	
	<i>Muhlenbergia racemosa</i>	Green muhly	5 (1)	11	17	
	<i>Panicum capillare</i>	Witchgrass	0 (1)	8	13	
	<i>Panicum virgatum</i>	Switchgrass	5 (5)	44	70	
	<i>Pascopyrum smithii</i>	Western wheatgrass	5	50	79	
	<i>Schedonnardus paniculatus</i>	Tumblegrass	1	1	2	
	<i>Schizachyrium scoparium</i>	Little bluestem	5 (5)	52	83	
<i>Setaria glauca</i>	Yellow foxtail	0 (1)	34	54		

APPENDIX 1. Continued.

Family	Latin Name	Common Name	C-value ^{ab}	No. of Sites of Occurrence	Frequency %
	<i>Setaria viridis</i>	Green foxtail	0 (1)	3	5
	<i>Sorghastrum nutans</i>	Indian grass	6 (5)	38	60
	<i>Spartina pectinata</i>	Prairie cordgrass	4 (4)	47	75
	<i>Sphenopobolis obtusata</i>	Prairie wedgegrass	7 (7)	1	2
	<i>Sporobolus asper</i>	Rough dropseed	6 (1)	5	8
	<i>Sporobolus cryptandrus</i>	Sand dropseed	6 (7)	18	29
	<i>Sporobolus heterolepis</i>	Prairie dropseed	10 (10)	39	62
	<i>Sporobolus neglectus</i>	Annual dropseed	0 (1)	1	2
	<i>Stipa comata</i>	Needle-and-thread	5 (1)	17	27
	<i>Stipa spartea</i>	Porcupine grass	7 (7)	46	73
	<i>Stipa viridula</i>	Green needlegrass	6 (1)	51	81
Polemoniaceae	<i>Phlox pilosa</i>	Downy phlox	8 (7)	1	2
Polygalaceae	<i>Polygala alba</i>	White milkwort	4	9	14
	<i>Polygala verticillata</i>	Annual milkwort	9 (9)	8	13
Polygonaceae	<i>Polygonum arenastrum</i>	Knotweed	0 (1)	1	2
	<i>Polygonum coccineum</i>	Water smartweed	4 (4)	2	3
	<i>Polygonum convolvulus</i>	Buckwheat	2 (1)	19	30
	<i>Polygonum lapathifolium</i>	Lady's thumb	0 (0)	4	6
	<i>Rumex mexicanus</i>	Willow-leaved dock	1 (1)	13	21
Portulacaceae	<i>Talinum parviflorum</i>	Prairie fameflower	8	1	2
Primulaceae	<i>Lysimachia ciliata</i>	Fringed loosestrife	4 (4)	4	6
Ranunculaceae	<i>Anemone canadensis</i>	Meadow anemone	4 (4)	38	60
	<i>Anemone cylindrica</i>	Thimble flower	7 (6)	44	70
	<i>Anemone patens</i>	Pasque flower, Crocus	8 (10)	34	54
	<i>Delphinium virescens</i>	Prairie larkspur	10	23	37
	<i>Ranunculus cymbalaria</i>	Seaside crowfoot	3 (5)	6	10
	<i>Ranunculus pensylvanicus</i>	Bristly crowfoot	6 (6)	3	5
	<i>Thalictrum dasycarpum</i>	Meadow rue	5 (5)	14	22
Rosaceae	<i>Agrimonia striata</i>	Striate agrimony	6	13	21
	<i>Fragaria virginiana</i>	Wild strawberry	6 (1)	14	22
	<i>Geum canadense</i>	White avens	1 (1)	1	2
	<i>Geum triflorum</i>	Prairie smoke	10 (10)	28	44
	<i>Potentilla anserina</i>	Silverweed	5 (6)	12	19
	<i>Potentilla arguta</i>	Tall cinquefoil	9 (9)	39	62
	<i>Potentilla norvegica</i>	Rough cinquefoil	0 (0)	18	29
	<i>Potentilla pensylvanica</i>	Pennsylvania cinquefoil	10 (10)	19	30
	<i>Potentilla recta</i>	Sulfur cinquefoil	5 (1)	1	2
	<i>Rosa arkansana</i>	Prairie rose	5 (5)	56	89
Rubiaceae	<i>Galium boreale</i>	Northern bedstraw	7 (7)	19	30
Santalaceae	<i>Comandra umbellata</i>	Bastard toadflax	7 (7)	10	16
Saxifragaceae	<i>Heuchera richardsonii</i>	Alumroot	8 (8)	11	17
Scrophulariaceae	<i>Agalinis aspera</i>		10 (10)	4	6
	<i>Castilleja sessiliflora</i>	Downy paintbrush	8 (10)	3	5
	<i>Orthocarpus luteus</i>	Owl clover	7	1	2
	<i>Pedicularis canadensis</i>	Common lousewort	9 (9)	4	6
	<i>Pedicularis lanceolata</i>		9 (9)	5	8
	<i>Penstemon albidus</i>	White beardtongue	8	5	8
	<i>Penstemon gracilis</i>	Slender beardtongue	7 (1)	9	14
	<i>Penstemon grandiflorus</i>	Large beardtongue	4 (1)	1	2
	<i>Scrophularia lanceolata</i>	Figwort	5 (5)	6	10
	<i>Veronicastrum virginicum</i>	Culver's root	10 (7)	1	2
Selaginellaceae	<i>Selaginella rupestris</i>	Rock spikemoss	10 (10)	1	2
Solanaceae	<i>Physalis heterophylla</i>	Clammy groundcherry	5 (3)	21	33
	<i>Physalis longifolia</i>	Common groundcherry	0 (0)	9	14
	<i>Physalis virginiana</i>	Virginia groundcherry	4 (4)	51	81
	<i>Solanum carolinense</i>	Carolina horse-nettle	0 (1)	1	2
	<i>Solanum ptycanthum</i>	Black nightshade	0 (0)	3	5
	<i>Solanum rostratum</i>	Buffalobur	0 (1)	4	6
	<i>Solanum triflorum</i>	Cut-leaved nightshade	0 (1)	1	2

APPENDIX 1. Continued.

Family	Latin Name	Common Name	C-value ^{ab}	No. of Sites of Occurrence	Frequency %
Verbenaceae	<i>Verbena bracteata</i>	Prostrate vervain	0 (0)	5	8
	<i>Verbena stricta</i>	Hoary vervain	4 (4)	51	81
Violaceae	<i>Viola pedatifida</i>	Prairie violet	8 (9)	39	62

^aC-values determined by Dr. Gary Larson (SDSU), David Ode (S.D. Game, Fish and Parks), Eric Fairlee (graduate student/summer technician, SDSU), and Jeremy Higgins (graduate student, SDSU) in collaboration

^bC-values in parentheses are from *Plants of the Chicago Region* (Swink and Wilhelm 1994). Those species without values in parentheses are not treated in that flora

APPENDIX 2. Introduced vascular plant species detected during inventories of 63 remnant tallgrass prairie tracts in South Dakota, 1998, and their frequencies. Introduced species are not assigned C-values.

Family	Scientific Name	Common Name	No. of Sites of Occurrence	Frequency %	
Asteraceae	<i>Arctium minus</i>	Common burdock	4	6	
	<i>Carduus acanthoides</i>	Plumeless thistle	9	14	
	<i>Carduus nutans</i>	Musk thistle	17	27	
	<i>Cirsium arvense</i>	Canada thistle	55	87	
	<i>Cirsium vulgare</i>	Bull thistle	35	56	
	<i>Sonchus arvensis</i>	Perennial sow-thistle	37	59	
	<i>Taraxacum officinale</i>	Common dandelion	36	57	
	<i>Tragopogon dubius</i>	Yellow goatsbeard	49	78	
	Brassicaceae	<i>Capsella bursa-pastoris</i>	Shepherd's purse	3	5
<i>Descurainia sophia</i>		Flixweed	13	21	
<i>Sisymbrium altissimum</i>		Tumbling mustard	7	11	
Cannabaceae	<i>Cannabis sativa</i>	Wild hemp	5	8	
Chenopodiaceae	<i>Chenopodium album</i>	Lambs-quarters	4	6	
	<i>Kochia scoparia</i>	Kochia	4	6	
	<i>Salsola collina</i>	Tumbleweed	7	11	
Euphorbiaceae	<i>Euphorbia esula</i>	Leafy spurge	14	22	
	<i>Euphorbia glyptosperma</i>	Ridge-seeded spurge	1	2	
Fabaceae	<i>Coronilla varia</i>	Crown vetch	2	3	
	<i>Medicago lupulina</i>	Black medic	39	62	
	<i>Medicago sativa</i>	Alfalfa	29	46	
	<i>Melilotus</i> spp.	White/Yellow sweetclover	56	89	
	<i>Trifolium pratense</i>	Red clover	19	30	
	<i>Trifolium repens</i>	White clover	30	48	
Lamiaceae	<i>Leonurus cardiaca</i>	Motherwort	1	2	
Lamiaceae	<i>Nepeta cataria</i>	Catnip	7	11	
Liliaceae	<i>Asparagus officinalis</i>	Asparagus	4	6	
Malvaceae	<i>Malva rotundifolia</i>	Common mallow	1	2	
Plantaginaceae	<i>Plantago major</i>	Common plantain	24	38	
Poaceae	<i>Agropyron cristatum</i>	Crest wheatgrass	11	17	
	<i>Alopecurus arundinaceus</i>	Creeping foxtail	1	2	
	<i>Bromus inermis</i>	Smooth brome	63	100	
	<i>Bromus japonicus</i>	Japanese brome	5	8	
	<i>Bromus tectorum</i>	Downy brome	3	5	
	<i>Echinochloa crusgalli</i>	Barnyard grass	1	2	
	<i>Elytrigia repens</i>	Quackgrass	52	83	
	<i>Eriochloa villosa</i>	Wooly cupgrass	1	2	
	<i>Pbleum pratense</i>	Timothy	26	41	
	<i>Poa compressa</i>	Canada bluegrass	19	30	
	<i>Poa pratensis</i>	Kentucky bluegrass	63	100	
	Polygonaceae	<i>Rumex crispus</i>	Sour dock	28	44
		<i>Rumex stenophyllus</i>		1	2
Scrophulariaceae		<i>Linaria vulgaris</i>	Butter-and-eggs	7	11
	<i>Verbascum thapsus</i>	Mullein	5	8	

Greenhouse Assessment of the Feeding Effects of *Galerucella* spp. (Coleoptera: Chrysomelidae) on Purple Loosestrife (*Lythrum salicaria*)

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Lythrum salicarium L. (purple loosestrife) is a Eurasian perennial that is spreading into wetlands and wet prairie meadows across much of North America. Colonization of wet meadows by purple loosestrife has generally been associated with a precipitous decrease in native flora and fauna. Several states, including Nebraska, have been introducing leaf-feeding beetles such as *Galerucella californiensis* and *Galerucella pusilla* (Coleoptera: Chrysomelidae) in an attempt to control this plant. This study addresses the impact that *Galerucella* spp. stocking densities has on stem growth and root starch storage in purple loosestrife. Plants were grown in a greenhouse with netting to maintain beetles on specific plants. At the end of each year: 1) leaves were randomly sampled from each plant to determine leaf surface area removed by beetle feeding; 2) fine roots were sampled and starch content was determined; and 3) stem regrowth was measured after winter. Our results indicated that increased beetle densities increased the leaf surface area removed but did not decrease the amount of starch storage in the roots or reduce regrowth. The use of *Galerucella* spp. as effective biocontrol agents for purple loosestrife on the Great Plains is questioned.

INDEX DESCRIPTORS: purple loosestrife, *Lythrum salicaria*, *Galerucella*, biological control.

Lythrum salicaria L. (purple loosestrife) arrived in North America in the early nineteenth century from Eurasia (Stuckey 1980) and now is an exotic wetland and wet meadow perennial responsible for the degradation of many prime habitats throughout the temperate regions of the United States and Canada (Malecki et al. 1993). Since its introduction along the eastern shores of North America, it has rapidly spread westward. The plant now occurs in dense stands throughout the northeastern United States, southeastern Canada, the Midwest, and in scattered locations in the western United States and southwestern Canada. The creation of irrigation systems in many western states has supported further establishment and spread of *L. salicaria* (Malecki et al. 1993). Invasion of *L. salicaria* into a wetland or wet meadow system reduces the extent of the native plant community and alters the native system's structure and function (Thompson et al. 1987).

A variety of characteristics exhibited by *L. salicaria* can cause its rapid spread. For example, a single, mature plant can produce more than 2.5 million seeds annually, and *Lythrum salicaria* has a perennial rootstock that annually sends up four to ten stems per root that grow to a height of up to two meters (McAvoy et al. 1997). The rootstock serves as a storage organ for starch, and starch is important as the storage carbohydrate in the roots and crown of *L. salicaria* (Katovich et al. 1999). The level of starch in roots is an indicator of plant stress, and severe leaf area reduction by phytophagous insects can result in a reduction in root starch levels (Parker 1970, Wargo 1972).

In North America there are no insects other than generalist feeders attacking *L. salicaria* (Hight 1990), and this has been a reason suggested for its spread. In order to control *L. salicaria*, four species of insects that are specialist feeders on *L. salicaria* in its native habitat were identified as potential biological control agents (Batra et al. 1986, Blossey and Schroeder 1986). *Galerucella californiensis* L. and *Galerucella pusilla* Duft are two of the species that have been approved by the United States Department of Agriculture for field release.

These small (3-5 mm), brown beetles defoliate *L. salicaria* as both adults and larvae. Further, they are univoltine with eggs laid on the plant and the larvae migrating to soil for pupation.

The objective of the present study was to examine the effects of various *Galerucella* spp. densities on *L. salicaria* growth, development and starch production in the greenhouse. This information could be used for management decisions for the control of *L. salicaria* invasion.

METHODS

In the spring of 1998, 26 mature *L. salicaria* root systems, at least one year of age and having a minimum of five previous-year shoots, were collected from a wet meadow along the Missouri River in Dixon County, Nebraska. The mature root systems were planted into standard greenhouse potting soil in 3-gallon pots, and the potted plants were placed in plastic wading pools with approximately 5 cm of standing water. The plants were maintained inside a greenhouse to prevent further spread of the plants. When the *L. salicaria* shoots grew to approximately 15 cm tall, testing began. Main stem length of all shoots of each plant was measured and then the plants were wrapped in a cloth screen. The screening was anchored to the pot, and the top of the screen was folded and sealed with tape to prevent beetles from escaping the enclosure.

Beetles used in this study were obtained from the U.S. Department of Agriculture (USDA) and contained a mixture of both *G. pusilla* and *G. californiensis*. The two species are indiscernible unless carefully examined using a microscope, and thus they are reared together by the USDA. Our use of this mixture mimics what is released for the control of *L. salicaria* in Nebraska.

Adult *Galerucella* spp. were then placed on the potted and screen-enclosed *L. salicaria*. Because the rootstocks were wild collected and of different sizes and presumably different ages, the individual plants had varying initial growth rates. To account for some of the variability inherent in initial plant size along with variation in plant age and growth prior to addition of the beetles and the genetic variation

between plants, the total number of beetles placed on each plant was not used. However, we calculated density of beetles stocked on each plant. The density of beetles was calculated as the number initially placed on the plant per cm of stem length, and this ranged from 0 (control) to 0.10 beetles/cm of stem length. The beetles were allowed to feed for three months prior to plant sampling. After the three months of feeding, twenty leaves from each plant were removed at random, all the stems from each plant were measured, and the lateral roots growing out of the drain holes of the pots were collected from each plant. The leaf samples were placed in a plant press and dried before analysis. The lateral root samples for starch determination were placed in zip-lock® bags and stored at -20°C .

Leaf area reduction was determined by using a scanning technique developed for this experiment. Due to time constraints, every other one of the twenty sampled leaves per plant was selected ($n = 10$) and scanned on a Hewlett-Packard ScanJet 4C flatbed scanner using Adobe PhotoShop v. 5.0 software. The leaves were scanned as a sharp black and white photo with 150-dpi \times 150-dpi sharpness. The leaf image was then saved and imported into Scion Image (<http://www.scioncorp.com>) where the area (mm^2) of the surface of each leaf was computed and recorded by Scion Image. The leaf surface area removed by beetle feeding was filled in digitally using Adobe PhotoShop, and then the surface area was re-measured. The area removed by beetle feeding was then calculated by subtracting the first area measurement from the second.

The lateral root samples were used to determine the starch content of the roots. The root samples were allowed to defrost, washed in distilled water and then dried at 75°C . The dried samples were then ground using a Wiley Mill with a 1 mm mesh screen. An Amylase/Amyloglucosidase detection method (Sigma Chemical Co., P.O. Box 14508, St. Louis, MO 63178, U.S.A. Kit STA-20) was used to determine the percent starch in the root samples.

The study was repeated again in 1999 with newly collected *L. salicaria*, and the same process was followed for planting, except a total of 25 plants were stocked with 50 beetles each and 25 plants were set aside as control on which no beetles were stocked. The beetle numbers were again calculated as beetles initially placed on the plant per cm of stem length because plants varied in size. This led to beetle density varying from 0 (control) to 0.17 beetles/cm of stem length. The plants were allowed to grow for three months before sampling. Sampling, processing and analysis followed the same protocol listed above.

Plants that died during the experiment were excluded from the data analyzed. All remaining data were analyzed using linear regression models and independent t-tests on arcsine transformed percentage data in Microsoft Excel.

RESULTS

Results from the 1998 Greenhouse Study

The beetle density was calculated as the amount of beetles/total stem length (cm) of the plants (range = 0 to 0.10 beetles/cm stem length). The control group of zero beetles had 0.00% leaf area reduction representing no feeding. The leaf surface area removed increased linearly as beetle density increased ($R^2 = 0.43$, $P = 0.003$, $y = 98.58 - 67.97x$, $n = 17$) (Fig. 1).

Higher densities of *Galerucella* spp. showed a slight increase in stem length per plant, but this relationship was not significant ($R^2 = 0.16$, $P = 0.102$, $y = 58.45x - 4876.34$) (Fig. 2). The number of new shoots that re-grew in 1999 showed a slight decrease with the stocking intensity from 1998, and this relationship was also not significant ($R^2 = 0.09$, $P = 0.133$, $y = 4.39 - 26.77x$, $n = 17$).

It was hypothesized that with an increase in leaf area reduction there would be a decrease in the percentage of starch present in the

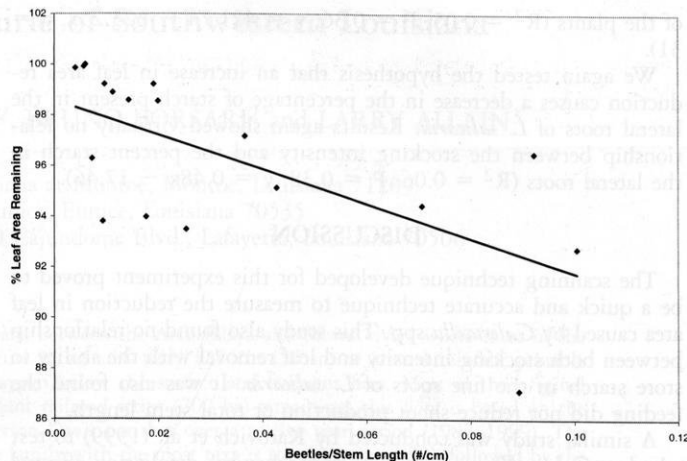


Fig. 1. *Lythrum salicaria* leaf area remaining after 3 months of feeding by varying densities of *Galerucella* spp. ($R^2 = 0.433$, $P = 0.003$, $y = 98.58 - 67.97x$) from the 1998 greenhouse study.

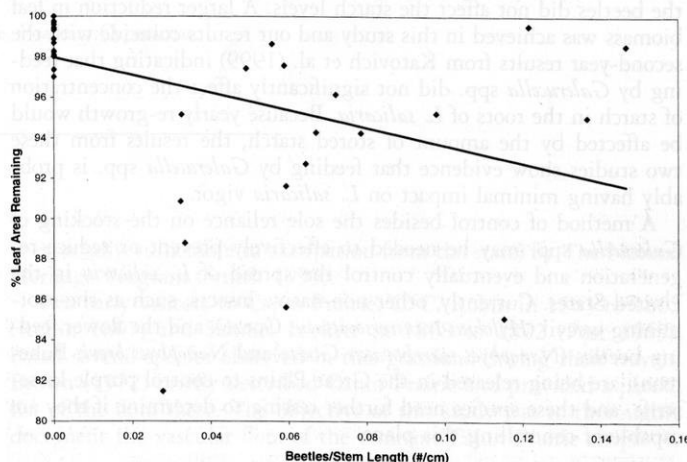


Fig. 2. *Lythrum salicaria* leaf area remaining after 3 months of feeding by varying densities of *Galerucella* spp. ($R^2 = 0.243$, $P = 0.0003$, $y = 93.79 - 290.64x$) from the 1999 greenhouse study.

fine roots of *L. salicaria*. However, our results showed virtually no relationship between stocking intensity and starch content of the roots ($R^2 = 0.01$, $P = 0.70$, $y = 41.08 - 0.249x$, $n = 17$). Therefore, starch in lateral roots was not consistently altered at any feeding intensity.

Results from the 1999 Greenhouse Study

The 25 plants in the control group had $97.2 (\pm 0.09 \text{ SD})\%$ of their original leaf area, whereas the 25 plants stocked with beetles had $93.2 (\pm 0.12 \text{ SD})\%$ of their original leaf area. The mean leaf surface remaining was significantly less on the plants with the beetles (independent t-test on arcsine transformed percentage data, $P = 0.002$) indicating that feeding by the beetles was causing the defoliation.

The data from the 1999 greenhouse study also showed a decrease in the percent of leaf area as the beetle/cm stem length intensity increased ($R^2 = 0.24$, $P = 0.0003$, $y = 93.79 - 290.64x$, $n = 31$) (Fig. 2), and, as in 1998, *Galerucella* spp. feeding effects showed only a slight, non-significant effect on reducing the total stem length

of the plants ($R^2 = 0.05$, $P = 0.36$, $y = 421.74 - 625.25x$, $n = 31$).

We again tested the hypothesis that an increase in leaf area reduction causes a decrease in the percentage of starch present in the lateral roots of *L. salicaria*. Results again showed virtually no relationship between the stocking intensity and the percent starch in the lateral roots ($R^2 = 0.06$, $P = 0.38$, $y = 0.48x - 17.46$).

DISCUSSION

The scanning technique developed for this experiment proved to be a quick and accurate technique to measure the reduction in leaf area caused by *Galerucella* spp. This study also found no relationship between both stocking intensity and leaf removal with the ability to store starch in the fine roots of *L. salicaria*. It was also found the feeding did not reduce shoot production or total stem length.

A similar study was conducted by Katovich et al. (1999) to test whether *Galerucella* spp. feeding or mechanical defoliation affected the starch and sucrose levels in the root and crown of *L. salicaria*. Initially, they discovered that the levels of starch in the roots and crowns of the plants stocked with *Galerucella* spp. were lower than the control group. However, when they retested the following year, the beetles did not affect the starch levels. A larger reduction in leaf biomass was achieved in this study and our results coincide with the second-year results from Katovich et al. (1999) indicating that feeding by *Galerucella* spp. did not significantly affect the concentration of starch in the roots of *L. salicaria*. Because yearly re-growth would be affected by the amount of stored starch, the results from these two studies show evidence that feeding by *Galerucella* spp. is probably having minimal impact on *L. salicaria* vigor.

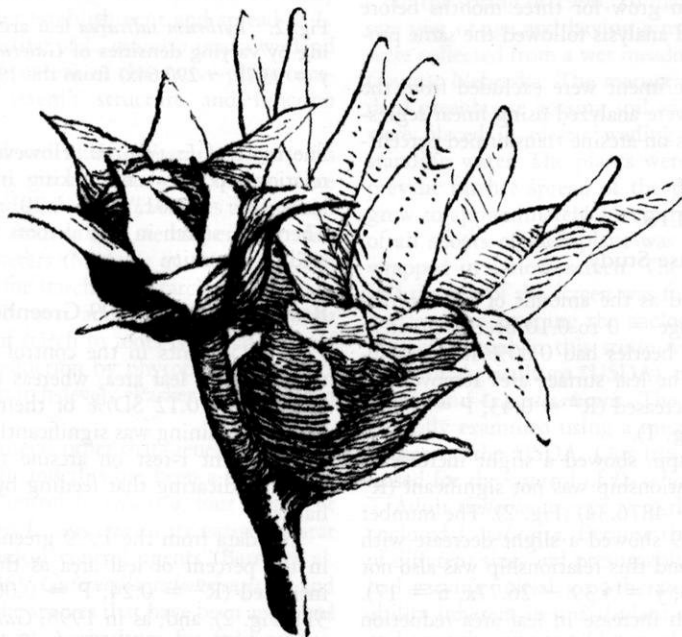
A method of control besides the sole reliance on the stocking of *Galerucella* spp. may be needed to effectively prevent or reduce regeneration and eventually control the spread of *L. salicaria* in the United States. Currently, other non-native insects, such as the root-mining weevil (*Hylobius transversovittatus* Goeze), and the flower feeding beetles (*Nanophyes marbovatus* Goeze and *Nanophyes brevis* Boheman); are being released in the Great Plains to control purple loosestrife, and these species need further testing to determine if they are capable of controlling this plant.

ACKNOWLEDGEMENTS

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Vascular Flora of the Cajun Prairie of Southwestern Louisiana

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Cajun Prairie is a Coastal Prairie developed in southwestern Louisiana between the Atchafalaya and Sabine rivers where most of the European settlers were Cajuns (French Acadians). This prairie occurs in an area with 125 cm (50 in) of annual rainfall; possible explanations for its development in this region include a hard claypan below the surface and frequent fires. Most of the original 1,000,000 ha of prairie have been destroyed with only a few remnant railroad strips (200 ha) remaining; this flora is based on the species observed in the remnant strips in Acadia, Allen, and Jefferson Davis parishes over a twelve year period (1987-1999). The vascular flora includes 512 taxa in 92 families and 277 genera. The family with the most taxa is the Asteraceae (80), followed by the Poaceae (78), Cyperaceae (50), Fabaceae (35), Lamiaceae (19), Scrophulariaceae (18), and Onagraceae (14). Some common Asteraceae taxa include *Arnoglossum plantagineum*, *Rudbeckia hirta*, *R. grandiflora*, *Silphium gracile*, *S. laciniatum*, *Solidago odora*, and several species of *Liatris* and *Symphotrichum*. Some common and conspicuous grass (Poaceae) species include *Andropogon gerardii*, *Panicum virgatum*, *Schizachyrium scoparium*, *Sorghastrum nutans*, and *Tripsacum dactyloides*. Other notable species include several species of *Baptisia*, *Dalea candida*, *Eryngium yuccifolium*, *Euphorbia corollata*, *Hedyotis nigricans*, and *Tephrosia onobrychoides*.

INDEX DESCRIPTORS: Louisiana flora, cajun prairie, Asteraceae, Poaceae, Cyperaceae.

Many authors map the southeastern extent of the true prairie in the United States in east Texas (Weaver 1954, Risser et al. 1981, Sims 1988, Kucera 1991). However, there is an area of remnant coastal tallgrass prairie in southwestern Louisiana between the Atchafalaya and Sabine rivers that has been called Attakapas Country, the Great Southwestern Prairie, or more recently, Cajun Prairie (Allen and Vidrine 1989). This grassland originally stretched across parts of Acadia, Allen, Calcasieu, Cameron, Evangeline, Iberia, Jefferson Davis, Lafayette, St. Landry, St. Martin, and Vermilion parishes. From 1869 to 1872, the prairie occupied an area of 1,000,000 ha (Post 1969).

Several interrelated factors help explain the presence of prairie in an area which receives an average of 125 cm of rainfall per year (National Oceanic and Atmospheric Administration 1987). The terrain is flat, and there is a densely-packed, hard clay pan located 20 to 40 cm below the surface (Clark et al. 1962, USDA 1970, Kilpatrick et al. 1980). Tree roots usually penetrate much deeper than roots of grasses and other herbaceous plants, but tree roots do not penetrate the clay pan (Brown 1972). Fires caused by lightning and later set by Indians and by European settlers also helped to retard the growth of trees (Allen and Vidrine 1989).

Today, most of the original prairie has been destroyed and replaced by cultivated crops, in particular rice. However, a few remnant prairies currently persist along railroad rights-of-way. Most of these remnants were never tilled or have not been tilled since the railroad acquired the land approximately 150 yrs ago. The remnants are all very narrow, mostly less than 30 m wide and no more than 800 m long. The estimated total area of intact Cajun Prairie today is 200 ha (Allen and Vidrine 1989). This ecosystem is ranked G2 (imperiled globally because of rarity or because of some factor(s) making it vulnerable to extirpation) by The Nature Conservancy (Grossman et al. 1994), and in Louisiana it is ranked S1 (critically imperiled in state because of extreme rarity or because of some factor(s) making

it especially vulnerable to extirpation from the state) by The Natural Heritage Program (Smith 1995).

Two early visitors to Cajun Prairie, C. C. Robin in 1803 to 1805 (Robin 1807) and Samuel Lockett in 1868 to 1872 (Post 1969), listed several species observed in this grassland during their travels. Brown (1972) briefly described Cajun Prairie and provided a partial list of the flora there. The objective of this study was to thoroughly document the vascular flora of the remnant Cajun Prairie strips.

STUDY AREA

Ten remnant strips were selected for this study based primarily on size and lack of disturbance. Each of the ten remnants was approximately 1,500 m long along railroad rights-of-way and consisted of two to four unbroken stretches. In the western and especially northwestern strips, there were small patches of pine savannah vegetation within the strips. Most of the remnant strips included small patches of disturbed vegetation within their boundaries. Five of the remnants were in Acadia Parish, three of which were along U.S. 90 between Estherwood and Mermentau, one along LA 91 south of Morse, and one west of LA 13 south of Eunice (Fig. 1). Four remnants were in Jefferson Davis Parish with three along U.S. 165 between Iowa and Kinder and one along U.S. 90 east of Elton. One remnant was in Allen Parish along U.S. 165 south of Kinder. The soils in these ten remnants were Crowley or Midland silt loam both with a clay hardpan (Clark et al. 1962, USDA 1970, Kilpatrick et al. 1980).

METHODS

The ten Cajun Prairie remnants were surveyed every two weeks from February to November, 1987, and the presence of all vascular plants was recorded. These ten remnants plus three other smaller remnant strips have been searched for taxa sporadically throughout

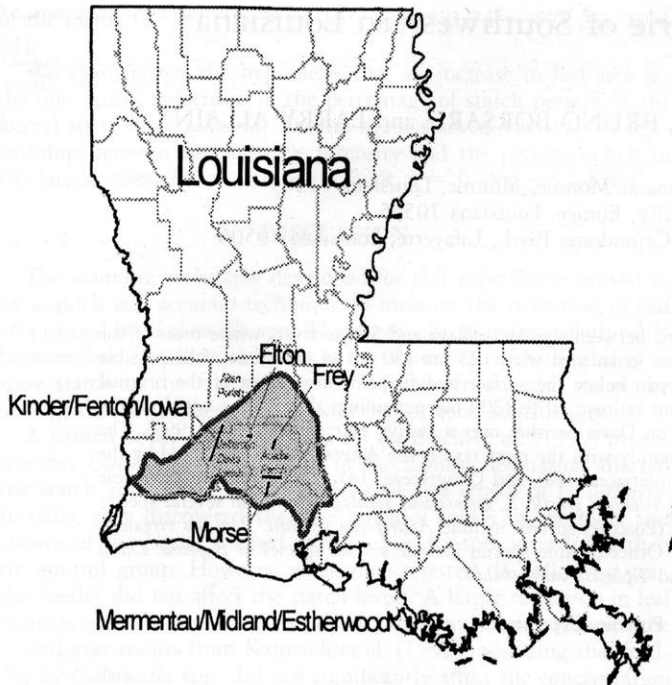


Fig. 1. Map of Louisiana with Cajun Prairie (shaded area) and ten remnant strips (dark lines).

the year from 1988 to present. Taxa were identified in the field by the senior author or keyed in the lab using the regional or state floras of Radford et al. (1968), Correll and Johnston (1970), or Allen (1992). For the less common taxa, herbarium specimens were collected and were deposited in the Herbarium of The University of Louisiana at Monroe (NLU). Notes were taken on abundance of each taxon; C (common) for those taxa that were observed in large numbers in almost all remnants, U (uncommon) for those taxa observed in small numbers in most remnants, and R (rare) for those taxa observed in small numbers in only one or two remnants (Appendix 1). The habitat within the remnant was also denoted; P (prairie), S (pine savannah), and D (disturbed areas). The atlases of Thomas and Allen (1993, 1996, 1998) were consulted to determine the native or introduced status of all taxa. Scientific names follow those in the Plants Database (USDA, NRCS 1999). To determine percent similarity, the list of Cajun Prairie plants was compared to similar lists from the Konza Prairie Research Natural Area in Kansas (Freeman and Hulbert 1985) and four Iowa prairies (Sorensen 1962, Crum 1972, Glenn-Lewin 1976, Wetzal et al. 1999).

RESULTS

A total of 512 taxa representing 92 families and 277 genera were identified from the ten remnant strips and/or other remnants (Appendix 1). The Asteraceae was the family with the most taxa 80 (15.62%) followed by Poaceae 78 (15.23%); Cyperaceae 50 (9.77%); Fabaceae 35 (6.84%); Lamiaceae 19 (3.71%); Scrophulariaceae 18 (3.51%); and Onagraceae 14 (2.73%). The most diverse genera were *Cyperus* and *Rhynchospora*, each with 12 taxa, and *Polygala* with nine. There were six genera with seven taxa each: *Asclepias*, *Carex*, *Dichanthelium*, *Eupatorium*, *Juncus*, and *Paspalum*. Most (482) of the 512 taxa were native (94.14%) with only 30 (5.86%) introduced taxa. Thirty-three (6.44%) taxa were noted in pine savannah vegetation and not a part of the prairie vegetation. A total of 235 taxa (45.90%) were identified from disturbed areas in the strips, especially along the

edges. The remaining taxa (244 taxa, 47.66%) constituted the Cajun Prairie Flora. Three hundred and thirty-nine (66.21%) taxa were rated uncommon in abundance and distribution while 44 (8.59%) were rare and 129 (25.19%) were common.

Common Asteraceae taxa occurring in these strips included *Arnoglossum plantagineum*, *Rudbeckia hirta*, *R. grandiflora*, *Silphium gracile*, *S. laciniatum*, *Solidago odora*, and several species of *Liatris* and *Symphoricarum*. Some common and obvious grass (Poaceae) species included *Andropogon gerardii*, *Panicum virgatum*, *Schizachyrium scoparium*, *Sorghastrum nutans*, and *Tripsacum dactyloides*. Other notable species included several species of *Baptisia*, *Dalea candida*, *Eryngium yuccifolium*, *Euphorbia corollata*, *Hedyotis nigricans*, and *Tephrosia onobrychoides*.

DISCUSSION

The Cajun Prairie Flora is based on the few remaining remnant strips and not the large contiguous vegetation that once covered the area. Our flora could be missing taxa that did not survive in the remnant strips but likewise could have additional taxa that prefer the edge and may not have been present in the original Cajun Prairie landscape.

The Louisiana Flora as reported by Thomas and Allen (1993, 1996, 1998) included 3249 taxa; 512 taxa (15.79%) were identified from the Cajun Prairie remnant strips. The 512 taxa (15.79%) is notable given the small total area of the remnant strips.

The comparison of this flora to other floras is difficult because most prairie studies do not include a comprehensive list of taxa (Anderson and Adams 1981, Smeins and Diamond 1983, Diamond and Smeins 1984, 1985, Kebart and Anderson 1987). The Konza Prairie Research Area in Kansas (Freeman and Hulbert 1985) included 441 species with 103 (20.12%) of those also found in the Cajun Prairie remnants. Of the 512 Cajun Prairie taxa, 62 (12.11%) were also listed for one or more Iowa prairies (Sorensen 1962, Crum 1972, Glenn-Lewin 1976, Wetzal et al 1999). Thus, the Cajun Prairie Flora is best described as a coastal plain flora overlaid with a major Midwestern prairie component.

The Cajun Prairie Habitat Preservation Society, U.S. Fish and Wildlife Service, USGS, and USDA/NRCS are pursuing preservation and restoration projects to protect this rapidly disappearing ecosystem. The oldest (1988) and best developed is in Eunice, Louisiana (Allen and Vidrine 1989).

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APPENDIX 1. List of taxa by major plant group and then by family from Cajun Prairie of southwestern Louisiana.

Key

* before name = introduced taxon

The first letter in parentheses after the name is the abundance rating where R = rare, U = uncommon, and C = common

The second letter in parentheses after the name is the habitat in the remnants where P = prairie, S = pine savannah, and D = disturbed area
The third superscripted letter, if present, in parentheses after the name indicates a report from Midwestern prairies where ^I = Iowa and ^K = Konza

PTERIDIOPHYTES

ASPLENIACEAE

Asplenium platyneuron (L.) B.S.P. (U,S)

DENNSTAEDTIACEAE

Pteridium aquilinum (L.) Kuhn (U,S)

LYGODIACEAE

**Lygodium japonicum* (Thunb. ex Murr.) Sw. (U,D)

GYMNOSPERMS

PINACEAE

Pinus palustris P. Mill. (R,S)

Pinus taeda L. (U,D)

TAXODIACEAE

Taxodium distichum (L.) L.C. Rich. (R,S)

MONCOTYLEDONS

AGAVACEAE

Manfreda virginica (L.) Salisb. ex Rose (C,P^K)

COMMELINACEAE

Commelina erecta L. (U,D)

Tradescantia hirsutiflora Bush (C,D)

Tradescantia virginiana L. (C,D^I)

CYPERACEAE

Bulbostylis capillaris (L.) Kunth ex C.B. Clarke (U,D)

Carex alata Torr. (U,D)

Carex albolutescens Schwein. (U,D)

Carex cherokeensis Schwein. (U,D)

Carex complanata Torr. & Hook. (U,D)

Carex frankii Kunth (U,D)

Carex microdonta Torr. & Hook. (U,P)

Carex vulpinoidea Michx. (C,D^I)

Cladium mariscus (L.) Pohl ssp. *jamaicense* (Crantz) Kükenth. (R,P)

Cyperus acuminatus Torr. & Hook. ex Torr. (C,D^I)

Cyperus croceus Vahl (U,D)

Cyperus echinatus (L.) Wood (R,D)

Cyperus erythrorhizos Muhl. (U,D)

Cyperus haspan L. (U,D)

**Cyperus iria* L. (U,D)

Cyperus oxylepis Nees ex Steud. (U,D)

Cyperus pseudovegetus Steud. (C,D)

Cyperus retrorsus Chapman (C,D)

**Cyperus rotundus* L. (U,D)

Cyperus strigosus L. (U,D^I)

Cyperus virens Michx. (C,D)

Eleocharis microcarpa Torr. (U,D)

Eleocharis montana (Kunth) Roemer & J.A. Schultes (C,D)

Eleocharis obtusa (Willd.) J.A. Schultes (C,D)

Eleocharis quadrangulata (Michx.) Roemer & J.A. Schultes (U,D)

Eleocharis tuberculosa (Michx.) Roemer & J.A. Schultes (U,S)

Fimbristylis autumnalis (L.) Roemer & J.A. Schultes (U,D)

Fimbristylis miliacea (L.) Vahl (U,D)

Fimbristylis puberula (Michx.) Vahl (U,P^K)

Fuirena pumila (Torr.) Spreng. (R,S)

Isolepis carinata Hook. & Arn. ex Torr. (U,D)

Kyllinga brevifolia Rottb. (U,D)

Kyllinga odorata Vahl (U,D)

Rhynchospora caduca Ell. (C,P)

Rhynchospora cephalantha Gray (C,P)

Rhynchospora chalarocephala Fern. & Gale (U,S)

Rhynchospora colorata (L.) H. Pfeiffer (R,P)

Rhynchospora corniculata (Lam.) Gray (C,D)

Rhynchospora elliottii A. Dietr. (C,P)

Rhynchospora globularis (Chapman) Small (C,P)

Rhynchospora glomerata (L.) Vahl (C,P)

Rhynchospora harveyi W. Boott (U,P)

Rhynchospora microcarpa Baldw. ex Gray (C,P)

Rhynchospora pusilla Chapman ex M.A. Curtis (U,P)

Rhynchospora rariflora (Michx.) Ell. (U,S)

- Scleria ciliata* Michx. (C,P)
Scleria pauciflora Muhl. ex Willd. (C,P)
Scleria reticularis Michx. (R,S)
Scleria verticillata Muhl. ex Willd. (R,S)
- IRIDACEAE
Herbertia labue (Molina) Goldblatt (R,P)
Iris virginica L. (U,P)¹
Sisyrinchium angustifolium P. Mill. (C,P)
Sisyrinchium atlanticum Bickn. (U,P)
Sisyrinchium exile Bickn. (C,D)
Sisyrinchium langloisii Greene (C,P)
- JUNCACEAE
Juncus brachycarpus Engelm. (C,D)
Juncus effusus L. (C,D)
Juncus marginatus Rostk. (C,P)
Juncus nodatus Coville (C,D)
Juncus polycephalus Michx. (C,D)
Juncus tenuis Willd. (C,D)¹
Juncus validus Coville (C,D)
- LILIACEAE
Alettris aurea Walt. (R,S)
Alettris farinosa L. (R,S)
Allium canadense L. var. *canadense* (C,D)¹ K
Allium canadense L. var. *mobile* (Regel) Ownbey (U,P)
Hymenocallis liriosme (Raf.) Shinnery (U,P)
Hypoxis hirsuta (L.) Coville (C,P)¹ K
Notboscordum bivalve (L.) Britt. (C,P)^K
- ORCHIDACEAE
Calopogon oklahomensis D.H. Goldman (R,P)
Platanthera nivea (Nutt.) Luer (R, S)
Pteroglossaspis ecristata (Fern.) Rolfe (R,P)
Spiranthes vernalis Engelm. & Gary (C,P)^K
- POACEAE
Agrostis hyemalis (Walt.) B.S.P. (C,P)¹ K
Alopecurus carolinianus Walt. (U,D)
Andropogon gerardii Vitman (C,P)¹ K
Andropogon glomeratus (Walt.) B.S.P. (C,P)
Andropogon gyrans Ashe var. *gyrans* (U,P)
Andropogon ternarius Michx. (U,P)
Andropogon virginicus L. (C,P)^K
Antbaenantia rufa (Nutt.) J.A. Schultes (U,P)
Aristida longispica Poir. var. *longispica* (U,D)^K
Aristida oligantha Michx. (U,D)
Aristida purpurascens Poir. var. *purpurascens* (C,P)^K
Axonopus fissifolius (Raddi) Kuhlman. (U,D)
Bothriochloa exaristata (Nash) Henr. (R,P)
**Bothriochloa ischaemum* (L.) Keng (U,D)
Bothriochloa longipaniculata (Gould) Allred & Gould (U,D)
Briza minor L. (U,D)
Bromus catharticus Vahl (U,D)
**Chloris canterai* Arech. (U,D)
Coelorachis cylindrica (Michx.) Nash (U,P)
Coelorachis rugosa (Nutt.) Nash (U,S)
Ctenium aromaticum (Walt.) Wood (U,S)
Cynodon dactylon (L.) Pers. (U,D)
Dichanthelium aciculare (Desv. ex Poir.) Gould & C.A. Clark (C,P)
Dichanthelium acuminatum (Sw.) Gould & C.A. Clark (C,P)¹ K
Dichanthelium dichotomum (L.) Gould var. *dichotomum* (U,P)^K
Dichanthelium oligosanthos (J.A. Schultes) Gould var. *scribnerianum* (Nash) Gould (C,P)¹ K
Dichanthelium ovale (Ell.) Gould & C.A. Clark (U,P)^K
Dichanthelium scoparium (Lam.) Gould (C,P)^K
Dichanthelium sphaerocarpon (Ell.) Gould var. *sphaerocarpon* (C,P)^K
Digitaria ciliaris (Retz.) Koel. (C,D)
Digitaria cognata (J.A. Schultes) Pilger (U,P)^K
Digitaria filiformis (L.) Koel. (U,P)^K
Digitaria ischaemum (Schreb.) Schreb. ex Muhl. (C,D)¹
Digitaria violascens Link (U,D)
Echinochloa crus-galli (L.) Beauv. (U,D)¹
Eragrostis bahiensis (Schrad. ex J.A. Schultes) J.A. Schultes (U,D)
Eragrostis elliottii S. Wats. (U,P)
- Eragrostis hirsuta* (Michx.) Nees (C,P)
Eragrostis lugens Nees (C,P)
Eragrostis refracta (Muhl.) Scribn. (C,P)
Eragrostis spectabilis (Pursh) Steud. (C,P)¹ K
Gymnopogon brevifolius Trin. (U,P)
Leersia bexandra Sw. (U,D)
Limodea arkansana (Nutt.) L.H. Dewey (U,D)
Lolium perenne L. (U,D)
Muhlenbergia capillaris (Lam.) Trin. (C,P)
Panicum anceps Michx. (C,P)
Panicum brachyanthum Steud. (U,P)
Panicum bemitomon J.A. Schultes (U,P)
Panicum rigidulum Bosc ex Nees var. *rigidulum* (U,D)
Panicum virgatum L. (C,P)¹ K
**Paspalum dilatatum* Poir. (U,D)
Paspalum floridanum Michx. (C,P)
Paspalum laeve Michx. (U,P)
Paspalum plicatulum Michx. (U,P)
Paspalum praecox Walt. (R,P)
Paspalum setaceum Michx. (C,P)¹ K
**Paspalum urvillei* Steud. (U,D)
Phalaris angusta Nees ex Trin. (U,D)
Phalaris caroliniana Walt. (U,D)
Schizachyrium scoparium (Michx.) Nash (C,P)¹ K
Schizachyrium tenerum Nees (C,P)
Setaria parviflora (Poir.) Kerguelen (U,D)
Setaria pumila (Poir.) Roemer & J.A. Schultes (U,D)¹
Sorghastrum nutans (L.) Nash (C,P)¹ K
**Sorghum halepense* (L.) Pers. (U,D)
Spartina spartinae (Trin.) Merr. ex A.S. Hitchc. (U,P)
Sphenopobolis obtusata (Michx.) Scribn. (C,P)¹ K
Sporobolus compositus (Poir.) Merr. (U,P)^K
**Sporobolus indicus* (L.) R. Br. (U,D)
Sporobolus junceus (Beauv.) Kunth (U,P)
Sporobolus silveanus Swallen (R,P)
Steinchisma bians (Ell.) Nash (C,D)
Tridens ambiguus (Ell.) J.A. Schultes (U,P)
Tridens strictus (Nutt.) Nash (C,P)
Tripsacum dactyloides (L.) L. (U,P)^K
Urochloa platyphylla (Munro ex Wright) R. Webster (U,D)
Vulpia octoflora (Walt.) Rydb. (U,D)
- PONTEDERACEAE
Pontederia cordata L. (U,P)^K
- SMILACACEAE
Smilax rotundifolia L. (U,D)
- TYPHACEAE
Typha latifolia L. (U,D)¹
- XYRIDACEAE
Xyris difformis Chapman var. *difformis* (U,S)
Xyris laxifolia Mart. (U,S)
Xyris torta Sm. (U,S)
- DICOTYLEDONS
- ACANTHACEAE
Hygrophila lacustris (Schlecht. & Cham.) Nees (U,P)
Justicia ovata (Walt.) Lindau (U,P)
Ruellia humilis Nutt. (C,P)¹ K
- AMARANTHACEAE
**Alternanthera philoxeroides* (Mart.) Griseb. (U,D)
- ANACARDIACEAE
Rhus copallinum L. (U,D)
Toxicodendron radicans (L.) Kuntze (U,D)¹
- APIACEAE
Centella erecta (L. f.) Fern. (U,P)
Chaerophyllum tainturieri Hook. (U,D)
Cicuta maculata L. (U,P)¹
Cynosciadium digitatum DC. (U,P)
Eryngium integrifolium Walt. (U,S)
Eryngium yuccifolium Walt. (U,S)
Polytaenia nuttallii DC. (U,P)
Ptilimnium capillaceum (Michx.) Raf. (C,D)
Ptilimnium costatum (Ell.) Raf. (U,S)

- Spermolepis echinata* (Nutt. ex DC.) Heller (U,D)
APOCYNACEAE
Amsonia tabernaemontana Walt. (U,P^K)
AQUIFOLIACEAE
Ilex decidua Walt. (U,D)
Ilex vomitoria Ait. (U,D)
ASCLEPIADACEAE
Asclepias lanceolata Walt. (U,P)
Asclepias longifolia Michx. (U,P)
Asclepias obovata Ell. (C,P)
Asclepias tuberosa L. (U,P^I K)
Asclepias verticillata L. (U,P^I K)
Asclepias viridiflora Raf. (U,P^I K)
Asclepias viridis Walt. (C,P^K)
Cynanchum laeve (Michx.) Pers. (U,D)
Matelea gonocarpus (Walt.) Shinnery (U,D)
ASTERACEAE
Ambrosia artemisiifolia L. (U,D^I)
Ambrosia bidentata Michx. (U,D)
Ambrosia psilostachya DC. (U,D^I)
Ambrosia trifida L. (U,D^I)
Arnoglossum plantagineum Raf. (U,P^I K)
Baccharis halimifolia L. (U,D)
Bidens aristosa (Michx.) Britt. (U,P^K)
Bigelovia virgata (Michx.) DC. (R,P)
Boltonia asteroides (L.) L'Hér. (C,P^K)
Boltonia diffusa Ell. (C,P)
Chromolaena vifolia (L.) King. & H.E. Robins. (U,P)
Chrysopsis mariana (L.) Ell. (U,P)
Cirsium horridulum Michx. (U,D)
Coryza canadensis (L.) Cronq. (U,D)
Coreopsis gladiata Walt. (C,P)
Coreopsis lanceolata L. (C,P^K)
Coreopsis pubescens Ell. (C,P)
Coreopsis tinctoria Nutt. (C,D)
Coreopsis tripteris L. (U,P^K)
Echinacea pallida (Nutt.) Nutt. (U,P^I)
Erechtites hieracifolia (L.) Raf. ex DC. (U,D^I)
Erigeron annuus (L.) Pers. (C,P^I K)
Erigeron philadelphicus L. (U,D)
Erigeron strigosus Muhl. ex Willd. (C,P^I K)
Eupatorium capillifolium (Lam.) Small (U,D)
Eupatorium hyssopifolium L. (C,P^K)
Eupatorium leucolepis (DC.) Torr. & Gray (U,S)
Eupatorium perfoliatum L. (U,P^I K)
Eupatorium rotundifolium L. (C,P)
Eupatorium semiserratatum DC. (U,P)
Eupatorium serotinum Michx. (U,D)
Eurybia hemispherica (Alexander) Nesom (U,P)
Euthamia leptoccephala (Torr. & Gray) Greene (C,P)
Euthamia tenuifolia (Pursh) Nutt. (U,P)
Gaillardia aestivalis (Walt.) H. Rock (U,P)
Gamochaeta purpurea (L.) Cabrera (U,D)
**Helenium amarum* (Raf.) H. Rock (U,D)
Helenium drummondii H. Rock (R,P)
Helenium flexuosum Raf. (C,P^K)
Helianthus angustifolius L. (C,P)
Helianthus mollis Lam. (C,P^K)
Iva annua L. (U,D)
Krigia caespitosa (Raf.) Chambers (U,D)
Krigia dandelion (L.) Nutt. (U,P^K)
Krigia virginica (L.) Willd. (U,D^I)
Lactuca canadensis L. (U,D^I)
Lactuca floridana (L.) Gaertn. (U,D^I)
Liatris acidota Engelm. & Gray (C,P)
Liatris elegans (Walt.) Michx. (U,P)
Liatris pycnostachya Michx. (C,P^I K)
Liatris spicata (L.) Willd. (C,P)
Liatris squarrosa (L.) Michx. (U,P^K)
Mikania scandens (L.) Willd. (U,D)
Oligoneuron nitidum (Torr. & Gray) Small (C,P)
Packera glabella (Poir.) C. Jeffrey (U,D)
Packera tomentosa (Michx.) C. Jeffrey (R,S)
Pityopsis graminifolia (Michx.) Nutt. (C,P)
Pluchea camphorata (L.) DC. (U,D)
Pluchea foetida (L.) DC. (U,D)
Pluchea rosea Godfrey (U,D)
Pseudognaphalium obtusifolium (L.) Hilliard & Burt (U,P^K)
Pterocaulon virgatum (L.) DC. (R,P)
Pyrrhopyppus carolinianus (Walt.) DC. (C,P^K)
Rudbeckia grandiflora (D. Don) J.F. Gmel. ex DC. (C,P)
Rudbeckia hirta L. (C,P^I K)
Rudbeckia texana (Perdue) P. Cox & Urbatsch (U,P)
Silphium gracile Gray (C,P)
Silphium laciniatum L. (U, P^I K)
Solidago canadensis L. (C,D^I K)
Solidago odora Ait. (C,P)
Solidago rugosa P. Mill. (U,P)
Solidago sempervirens L. var. *mexicana* (L.) Fern. (U,P)
Sonchus asper (L.) Hill (U,D)
Sonchus oleraceus L. (U,D)
Symphytotrichum dumosum (L.) Nesom (C,P^K)
Symphytotrichum lateriflorum (L.) A. & D. Löve (C,P^K)
Symphytotrichum oolentangiense (Riddell) Nesom (U,P^I K)
Symphytotrichum patens (Ait.) Nesom (C,P^K)
Symphytotrichum pratense (Raf.) Nesom (U,P)
Vernonia gigantea (Walt.) Trel. (U,P)
Vernonia texana (Gray) Small (U,P)
BIGNONIACEAE
Campsis radicans (L.) Seem. ex Bureau (U,D)
BORAGINACEAE
Myosotis verna Nutt. (U,D)
BRASSICACEAE
Cardamine hirsuta L. (U,D)
Cardamine parviflora L. var. *arenicola* (Britt.) O.E. Schulz (U,D)
Lepidium virginicum L. (U,D^I)
BUDDLEJACEAE
Polyprenum procumbens L. (C,D)
CALLITRICHACEAE
Callitriche heterophylla Pursh (U,D)
CAMPANULACEAE
Lobelia appendiculata A. DC. (C,P)
Lobelia puberula Michx. (C,P)
Triodanis perfoliata (L.) Nieuwl. (U,D^I)
CAPRIFOLIACEAE
**Lonicera japonica* Thunb. (U,D)
Sambucus nigra L. ssp. *canadensis* (L.) R. Bolli (U,D^I)
CARYOPHYLLACEAE
Cerastium glomeratum Thuill. (U,D)
Silene antirrhina L. (U,D)
CISTACEAE
Lechea mucronata Raf. (U,P^K)
Lechea tenuifolia Michx. (U,P^K)
CLUSIACEAE
Hypericum crux-andreae (L.) Crantz (U,P)
Hypericum drummondii (Grev. & Hook.) Torr. & Gray (U,D)
Hypericum gentianoides (L.) B.S.P. (U,D)
Hypericum gymnanthum Engelm. & Gray (U,D)
Hypericum hypericoides (L.) Crantz ssp. *hypericoides* (U,P)
Hypericum nudiflorum Michx. ex Willd. (U,P)
CONVOLVULACEAE
Dichondra carolinensis Michx. (U,D)
Ipomoea lacunosa L. (U,D)
Ipomoea sagittata Poir. (U,P)
Stylisma aquatica (Walt.) Raf. (R,P)
CORNACEAE
Cornus drummondii C.A. Mey. (U,D^I)
CUCURBITACEAE
**Cucumis melo* L. (U,D)
Melothria pendula L. (U,D)
CUSCUTACEAE
Cuscuta indecora Choisy (U,P)

DROSERACEAE

Drosera brevifolia Pursh (U,S)

EBENACEAE

Diospyros virginiana L. (U,D)

ERICACEAE

Vaccinium arboreum Marsh. (U,D)

EUPHORBIACEAE

Acalypha gracilens Gray (C,P^K)*Caperonia palustris* (L.) St.-Hil. (U,D)*Chamaesyce humistrata* (Engelm.) Small (U,D)*Chamaesyce maculata* (L.) Small (U,D¹)**Chamaesyce nutans* (Lag.) Small (U,D¹)*Croton capitatus* Michx. (C,D)*Croton glandulosus* L. (U,D)*Croton willdenowii* G.L. Webster (U,P^K)*Euphorbia corollata* L. (C,P¹ K)*Euphorbia spatbulata* Lam. (U,D)*Tragia betonicifolia* Nutt. (U,P)**Triadica sebifera* (L.) Small (U,D)

FABACEAE

Aeschynomene indica* L. (U,D)*Baptisia alba* (L.) Vent. (U,P¹ K)*Baptisia bracteata* Muhl. ex Ell. var. *laevicaulis* (Gray ex Canby) Isely (U,P)*Baptisia bracteata* Muhl. ex Ell. var. *leucophaea* (Nutt.) Kartesz & Gandhi (U,P¹ K)*Baptisia nuttalliana* Small (R,S)*Baptisia sphaerocarpa* Nutt. (U,P)*Centrosema virginianum* (L.) Benth. (U,P)*Chamaecrista fasciculata* (Michx.) Greene (C,P¹ K)*Crotalaria sagittalis* L. (U,P^K)*Dalea candida* Michx. ex Willd. (U,P¹ K)*Desmodium ciliare* (Muhl. ex Willd.) DC. (U,P)*Desmodium paniculatum* (L.) DC. (U,P^K)*Desmodium sessilifolium* (Torr.) Torr. & Gray (U,P^K)*Galactia volubilis* (L.) Britt. (U,P)Glottidium vesicarium* (Jacq.) Harper (U,D)**Kummerowia striata* (Thunb.) Schindl. (U,D)*Lepedeza capitata* (Michx.) (U,P¹ K)*Lepedeza repens* (L.) W. Bart. (U,P^K)*Lepedeza virginica* (L.) Britt. (U,P^K)**Medicago lupulina* L. (U,D¹)**Medicago polymorpha* L. (U,D)**Melilotus indicus* (L.) All. (U,D)*Mimosa microphylla* Dry. (C,P)*Neptunia lutea* (Leavenworth) Benth. (U,P)*Neptunia pubescens* Benth. (U,P)*Orbexilum pedunculatum* (P. Mill.) Rydb. var. *psoraloides* (Walt.) Isley (U,P)*Orbexilum simplex* (Nutt. ex Torr. & Gray) Rydb. (U,P)*Rhynchosia minima* (L.) DC. (R,D)*Strophostyles umbellata* (Muhl. ex Willd.) Britt. (C,P)*Stylosanthes biflora* (L.) B.S.P. (C,P)*Tephrosia onobrychoides* Nutt. (C,P)*Trifolium bejariense* Moric. (U,D)**Trifolium dubium* Sibthorp (U,D)**Trifolium resupinatum* L. (U,D)*Vicia ludoviciana* Nutt. (U,D)

FAGACEAE

Castanea pumila (L.) P. Mill. var. *pumila* (U,P)*Quercus falcata* Michx. (U,D)*Quercus incana* Bartr. (U,D)*Quercus marilandica* Muenchh. (U,D)*Quercus nigra* L. (U,D)*Quercus stellata* Wangenh. (U,D)*Quercus virginiana* P. Mill. (U,D)

GENTIANACEAE

**Centaurium pulchellum* (Sw.) Druce (U,D)*Sabatia brachiata* Ell. (U,S)*Sabatia campestris* Nutt. (U,P^K)*Sabatia gentianoides* Ell. (U,S)*Sabatia stellaris* Pursh (U,P)

GERANIACEAE

Geranium carolinianum L. (U,D¹)

HALORAGACEAE

Proserpinaca palustris L. (U,P^K)

HAMAMELIDACEAE

Liquidambar styraciflua L. (U,D)

HYDROPHYLLACEAE

Hydrolea ovata Nutt. ex Choisy (C,P)

JUGLANDACEAE

Carya illinoensis (Wangenh.) K. Koch (U,D)

LAMIACEAE

Hyptis alata (Raf.) Shinnars (U,P)*Lamium amplexicaule* L. (U,D)*Lycopus americanus* Muhl. ex W. Bart. (R,P¹ K)*Monarda fistulosa* L. (C,P¹ K)*Monarda lindheimeri* Engelm. & Gray ex Gray (U,P)*Monarda punctata* L. (U,P^K)*Phystostegia intermedia* (Nutt.) Engelm. & Gray (U,P)*Phystostegia virginiana* (L.) Benth. ssp. *praemorsa* (Shinnars) Cantino (U,P^K)**Prunella vulgaris* L. (C,D)*Pycnanthemum albescens* Torr. & Gray (U,P)*Pycnanthemum muticum* (Michx.) Pers. (U,P)*Pycnanthemum tenuifolium* Schrad. (C,P^K)*Salvia azurea* Michx. ex Lam. (C,P^K)*Salvia lyrata* L. (C,D)*Scutellaria integrifolia* L. (C,P)*Scutellaria parvula* Michx. (U,P^K)*Stachys crenata* Raf. (U,D)**Stachys floridana* Shuttlw. ex Benth (R,D).*Teucrium canadense* L. (C,P)

LAURACEAE

Sassafras albidum (Nutt.) Nees (U,D)

LENTIBULARIACEAE

Pinguicula pumila Michx. (R,S)*Utricularia subulata* L. (R,S)

LINACEAE

Linum medium (Planch.) Britt. var. *texanum* (Planch.) Fern. (C,P^K)*Linum sulcatum* Riddell (R,P^K)

LOGANIACEAE

Mitreola petiolata (J.F. Gmel.) Torr. & Gray (U,P)*Mitreola sessilifolia* (J.F. Gmel.) G. Don (U,P)

LYTHRACEAE

Cuphea glutinosa Cham. & Schlecht. (R,P)*Lythrum alatum* Pursh var. *lanceolatum* (Ell.) Torr & Gray ex Rothrock (C,P)

MALVACEAE

Callirhoe papaver (Cav.) Gray (U,P)*Hibiscus moscheutos* L. ssp. *lasiocarpus* (Cav.) O.J. Blanchard (U,P)*Modiola caroliniana* (L.) G. Don (U,D)*Sida rhombifolia* L. (U,D)

MELASTOMATACEAE

Rbxia mariana L. (C,P)

MELIACEAE

**Melia azedarach* L. (U,D)

MOLLUGINACEAE

**Mollugo verticillata* L. (U,D)

MYRICACEAE

**Morella cerifera* (L.) Small (U,P)

NYSSACEAE

Nyssa sylvatica Marsh (U,D)

OLEACEAE

**Ligustrum sinense* Lour. (U,D)

ONAGRACEAE

Gaura lindheimeri Engelm. & Gray (C,P)*Gaura longiflora* Spach (C,P^K)*Ludwigia decurrens* Walt. (U,D)*Ludwigia glandulosa* Walt. (U,D)*Ludwigia hirtella* Raf. (U,P)*Ludwigia leptocarpa* (Nutt.) Hara (U,D)*Ludwigia linearis* Walt. (C,P)*Ludwigia palustris* (L.) Ell. (U,D)*Oenothera biennis* L. (U,P^K)*Oenothera laciniata* Hill (U,D)

- Oenothera linifolia* Nutt. (U,D)
Oenothera pilosella Raf. ssp. *sessilis* (Pennell) Straley (R,P)
Oenothera spachiana Torr. & Gray (R,P)
Oenothera speciosa Nutt (U,D)
- OXALIDACEAE**
Oxalis stricta L. (U,D)
Oxalis violacea L. (U,P^K)
- PASSIFLORACEAE**
Passiflora incarnata L. (C,P)
- PHYTOLACCACEAE**
Phytolacca americana L. (U,D)
- PLANTAGINACEAE**
Plantago aristata Michx. (U,D)
Plantago heterophylla Nutt. (U,D)
Plantago virginica L. (C,D)
- POLEMONIACEAE**
Phlox pilosa L. (C,P^K)
- POLYGALACEAE**
Polygala cruciata L. (R,S)
Polygala incarnata L. (U,P^K)
Polygala leptocaulis Torr. & Gray (U,P)
Polygala mariana P. Mill. (C,P)
Polygala nana (Michx.) DC. (R,S)
Polygala ramosa Ell. (R,S)
Polygala sanguinea L. (U,P^K)
Polygala verticillata L. (U,P^K)
- POLYGONACEAE**
Polygonum hydropiperoides Michx. (C,D)
Rumex verticillatus L. (U,D)
- PORTULACACEAE**
Claytonia virginica L. (R,P^K)
- PRIMULACEAE**
Anagallis arvensis L. (U,D)
Anagallis minima (L.) Krause (U,D)
- RANUNCULACEAE**
Anemone caroliniana Walt. (R,P^K)
Ranunculus fascicularis Muhl. ex Bigelow (U,P^K)
Ranunculus laxicaulis (Torr. & Gray) Darby (U,D)
Ranunculus muricatus L. (U,D)
Ranunculus pusillus Poir. (U,D)
- RHAMNACEAE**
Berberia scandens (U,D)
Ceanothus americanus L. (U,P^K)
- ROSACEAE**
Crataegus crus-galli L. (U,D)
Geum canadense Jacq. (U,D)
Prunus serotina Ehrh. (U,D)
Rubus argutus Link (U,P)
Rubus trivialis Michx. (U,P)
- RUBIACEAE**
Cephalanthus occidentalis L. (U,D)
Diodia teres Walt. (U,D)
Diodia virginiana L. (U,D)
Galium aparine L. (U,D)
Galium tinctorium L. (U,D)
Galium virgatum Nutt. (R,P)
Hedyotis nigricans (Lam.) Fosberg (C,P^K)
Houstonia micrantha (Shinners) Terrell (U,D)
Oldenlandia boscii (DC.) Chapman (U,D)
- RUTACEAE**
Zanthoxylum clava-berculis L. (U,D)
- SALICACEAE**
Salix nigra Marsh. (U,D)
- SAPINDACEAE**
Cardiospermum halicacabum L. (U,D)
- SAXIFRAGACEAE**
Lepuropetalon spathulatum Ell. (U,D)
- SCROPHULARIACEAE**
Agalinis fasciculata (Ell.) Raf. (C,D)
Agalinis heterophylla (Nutt.) Small ex Britt. (U,D)
Agalinis oligophylla Pennell (U,P)
Agalinis skinneriana (Wood) Britt. (U,P^K)
Agalinis viridis (Small) Pennell (U,P)
Bacopa rotundifolia (Michx.) Wettst. (U,D)
Buchnera americana L. (C,P)
Gratiola neglecta Torr. (U,P^K)
Gratiola virginiana L. (U,D)
Lindernia dubia (L.) Pennell var. *dubia* (U,D)
Mecardonia acuminata (Walt.) Small (C,P)
Nuttallanthus canadensis (L.) D.A. Sutton (U,D)
Nuttallanthus texanus (Scheele) D.A. Sutton (U,D)
Pedicularis canadensis L. (R,P^K)
Penstemon digitalis Nutt. ex Sims (U,P^K)
Penstemon laxiflorus Pennell (U,P)
Veronica arvensis L. (U,D)
Veronica peregrina L. (U,D)
- SOLANACEAE**
Physalis angulata L. (U,D)
Physalis heterophylla Nees (U,P^K)
Solanum americanum P. Mill. (U,D)
Solanum carolinense L. (U,D)
Solanum dimidiatum Raf. (R,D)
Solanum elaeagnifolium Cav. (U,D)
- STERCULIACEAE**
 **Melochia corchorifolia* L. (U,D)
- STYRACACEAE**
Styrax americanus Lam. (U,P)
- ULMACEAE**
Celtis laevigata Willd. (U,D)
Ulmus americana L. (U,D)
- URTICACEAE**
Boehmeria cylindrica (L.) Sw. (U,S)
- VALERIANACEAE**
Valerianella radiata (L.) Dufr. (C,D)
- VERBENACEAE**
Glandularia pulchella (Sweet) Troncoso (U,D)
Phyla nodiflora (L.) Greene (U,D)
Verbena bonariensis L. (R,D)
Verbena brasiliensis Vell. (C,D)
Verbena halei Small (C,D)
Verbena litoralis Kunth (U,D)
- VIOLACEAE**
Viola lanceolata L. (R,P^K)
Viola sagittata Ait (R,P^K)
- VITACEAE**
Ampelopsis arborea (L.) Koehne (U,D)
Parthenocissus quinquefolia (L.) Planch. (U,D)
Vitis cinerea (Engelm.) Millard (U,D)

Preliminary Examination of Species of an Abandoned Farm Field in Tallgrass Mixed Hardwood Forest in Ottertail County, Minnesota

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Understanding the species composition of abandoned fields is useful for prairie restoration. Native prairie species that have survived farming practices, neglect, and competition from introduced species may be candidates for restoration. The objective of this study was to determine incidence and composition of native and introduced species in an abandoned farm field in Minnesota during two summer field seasons toward the ultimate goal of prairie restoration.

Ecology and species composition of an abandoned farm field in tallgrass-mixed oak hardwood forest region of Ottertail County, Minnesota were examined in summer, 1998 and 1999. This field was last farmed 30 years ago. To the north and east was a mixed hardwood forest, a playground was located to the west, and a gravel road with residences and a lake was to the north. The field was bisected by an undeveloped farm road and had sand-gravel soil. Transects were set up and species were recorded. At the edge of the forest, raspberries and prickly ash had begun to invade, and isolated box elder and oak had become established in the field. One bur oak (*Quercus macrocarpa* Michx.) was removed fall, 1998. In this field, the predominant species was smooth brome (*Bromus inermis* Leyss. subsp. *inermis*). Incidence of grasses and forbs were recorded and rated as to their suitability for inclusion in a prairie restoration project.

INDEX DESCRIPTORS: prairie plants, native plants, introduced plants.

The tallgrass prairie of the northern Great Plains extends from Manitoba south through parts of North Dakota, South Dakota, Nebraska, Kansas, Oklahoma, Minnesota, Wisconsin, Iowa, Illinois, Missouri, and Texas, with isolated patches in Ohio, Kentucky, Tennessee, Arkansas and Louisiana. (Great Plains Flora Association 1986, Madson and Oberle 1993, Weaver and Fitzpatrick 1934.) The prairie ecosystem is characterized by a predominance of grasses and is based, in part, upon climate in the form of annual precipitation. In Minnesota, precipitation occurs throughout the year with the greatest amount as rainfall occurring during summer months (Great Plains Flora Association 1986, Weaver 1954, Midwestern Regional Climate Center Database 2000).

As Weaver (1954) pointed out, little is known of the flora of the tallgrass prairie in northern Minnesota prior to the arrival of settlers who introduced agriculture and removed the prairie sod in the process. Although Moyer (1910) described the flora of southwestern Minnesota, the flora of northwestern Minnesota was not closely examined until fourteen years later by Ewing (1924), who described a brush-prairie transitional region that was located between deciduous forest and prairie. Ewing (1924) described the major grasses as Junegrass (*Koeleria cristata* Pers.), little bluestem (*Schizachyrium scoparium* Michx.), and prairie dropseed (*Sporobolus heterolepis* A. Gray).

More recently, Inouye et al. (1987) examined 22 abandoned farm fields ranging from 1 to 56 yrs since abandonment. The study sites were on sandy soils in the Cedar Creek Natural History Area of eastern Minnesota. The sandy soils were nutrient depleted, yet, with age, showed an increase in total soil nitrogen. This increase in soil nitrogen was correlated with an increase in vegetation cover, total above ground biomass and plant litter. Conversely, light penetration to the ground was decreased. They concluded that species richness per field and within field heterogeneity composition of species increased with age of field. In a follow-up study, Gleeson and Tilman (1990) reported that for nutrient-poor sandy soils, the pattern of

secondary succession differs from that of nutrient-rich soils. More recently, Tilman et al. (1994) reported that ecosystems at the prairie-forest border are highly sensitive to climatic variation, and their responses to climatic variation depend on biodiversity.

Brucker and Yang (1998) have applied these concepts to prairie restoration and their studies of sustaining natural ecosystems on the landscape scale. They suggested that understanding species composition is important for prairie restoration and will allow for a choice of plant species that are well adapted for a given location as well as for selection of species that have a reasonable chance of survival within microclimates of the site. Therefore, on prairie sites that have been disrupted by agricultural practices, those plant species that have survived farming practices, neglect, and competition from undesirable introduced species are candidates for inclusion in restoration.

While restoration projects often involve burning to maintain native species (Tilman et al. 1994), because of preferences of the owners of the land in this study, burning was not an option. Therefore, the objectives of this study were to: 1) design and implement a study to determine species composition, incidence, and frequency of plants on an abandoned farm field at a tallgrass prairie-oak forest interface in Minnesota; and 2) to identify native species growing in the field that were considered suitable candidates for prairie restoration.

METHODS

Description of Study Site

This study took place during 1998 and 1999 on privately owned land in Ottertail County in west central Minnesota. The prairie consisted of patches, large and small, that were adjacent to mixed hardwood oak forest and lakes. Ottertail County is characterized by the presence of numerous lakes, and the soil type ranges from rich dark loam to sandy.

The site had a soil type characterized as Hubbard-Duelm-Nidaaros

Table 1. Analysis of variance of annual and perennial species from an abandoned farm field in Ottertail County, Minnesota. Data were collected summer 1998 and summer 1999.

ANOVA						
Source of Variation	SS	df	MS	F	P	F crit
Between Groups	2102995.557	1	2102996	1.103573	0.297202	3.981896
Within Groups	129582489.1	68	1905625			
Total	131685484.6	69				

Table 2. Analysis of variance of introduced annual, introduced perennial, native annual, and native perennial species from an abandoned farm field in Ottertail County, Minnesota. Data were collected summer 1998 and summer 1999.

ANOVA						
Source of Variation	SS	df	MS	F	P	F crit
Between Groups	4332207.942	3	1444069	0.65897	0.580633	2.763556
Within Groups	127101333.2	58	2191402			
Total	131433541.2	61				

Table 3. Analysis of variance of forbs, grasses, shrubs and trees from an abandoned farm field in Ottertail County, Minnesota. Data were collected summer 1998 and summer 1999.

ANOVA						
Source of variation	SS	df	MS	F	P	F crit
Between Groups	10926538	1	10926538	5.706873	0.019906	3.993364
Within Groups	1.21E + 08	63	1914628			
Total	1.32E + 08	64				

associated soil with a texture of coarse sand (United States Department of Agriculture, Soil Survey of Ottertail County Minnesota 2000). The field was last farmed 30 years ago, and farming practices included crop production and animal husbandry. The field had not been grazed, hayed, or otherwise farmed since. Because of invasion by species from the adjoining forest, the field was a small patch, not quite rectangular in shape, approximately 80 × 60 m. The land sloped gently from north and east to south and west, and low spots occurred to the south-west and west. To the north and east was mixed hardwood oak forest, a privately-owned playground was located to the west, and a gravel road with residences and a lake was to the south. This field was bisected by an undeveloped farm road that runs north south. In summer 1988, the county graded and resurfaced the gravel road at the southern boundary and replanted the ditches using a Minnesota reseeding mix 50B consisting in part of smooth brome (*Bromus inermis* Leyss. subsp. *inermis*) and alfalfa (*Medicago sativa*) (Minnesota Department of Transportation Seeding Manual 2000).

Data Collection and Handling

Four transects, 60 m in length, were set up at 15 m intervals from the eastern to the western boundaries of this field. These transects divided the field into four roughly equivalent sections. Each transect was divided into 1 m segments, and plant species were recorded in alternating segments. For each 3 m along a transect, plants were recorded from 1 m. This was repeated along each transect for a total of 20 m along each transect. Plants were recorded if the

canopy was within 0.5 m of the transect. The species were recorded at two- to three-week intervals mid-May to July. Plant species observed were categorized as tree, grass or forb, native or introduced, and annual, perennial or biennial.

To determine if the frequency of the above categories of plants was significant, the data were examined by analysis of variance (ANOVA) (Ott 1993). All data analyses were performed using the data analysis function of Microsoft Excel software. A $P \leq 0.05$ was accepted as significant.

RESULTS

From this site, 70 species were recorded representing 27 plant families (Appendix 1). Of these, 52% were introduced and 48% were native. From the ANOVA comparing the annual and perennial species ($P = 0.2970$), the results were not significant (Table 1). Similarly, from an ANOVA comparing frequency of introduced annual, introduced perennial, native annual, and native perennial species ($P = 0.5803$), the results were not significant (Table 2). Conversely, from ANOVA comparing frequency of forbs and grasses (Table 3), the results were significant ($P = 0.0199$).

Of the species recorded in this study 52% were native and represented eighteen families. Of these, a subset representing 13 families and of 24 species was considered for inclusion in restoration efforts (Appendix 1).

The Minnesota Department of Transportation has a program to replant roadsides that have been under construction (Minnesota Department of Transportation 2000). In summer 1998, when the coun-

ty graded the gravel road, created drainage ditches, and reseeded, the smooth sumac that was located between the playground and gravel road was introduced along the ditch and began spreading into the field. In addition, seeding mixes (mix 50B) that were used in 1998 included introduced species smooth brome and alfalfa (Minnesota Department of Transportation Seeding Manual 2000).

DISCUSSION

Of the 70 species recorded in this 30 yr field in Ottertail County, Minnesota, both introduced and native plant species were represented (Appendix 1). Each of the native species had previously been reported in Minnesota, and none were rare or endangered (Great Plains Flora Association 1986, United States Department of Agriculture, Natural Resources Conservation Service Plants Database 2000).

From analysis of variance comparing the frequency of annual and perennial species (Table 1, $P = 0.2970$), the results were not significant, nor were the results of the comparison of the frequency of introduced annual, introduced perennial, native annual, and native perennial species (Table 2, $P = 0.5803$). Although this study did not report percent cover, these results were consistent with results reported by Inouye et al. (1987). In their study of abandoned fields with sandy soil, a decrease in percent cover by annual plants and an increase in percent cover by perennial plants was reported for fields from 1 yr to 60 yrs after abandonment. At approximately 20 yrs, a transition from a predominance of annual plants to a predominance of perennial occurred. In addition, they stated that conditions, and, therefore, results, may vary for other fields. In the current study, the field had been abandoned for 30 yrs and may be following a similar pattern of succession but on a slightly different timescale. Finally, in this current study, a significant difference was reported for grasses and forbs (Table 3, $P = 0.0199$). These results were also in agreement with a decrease in percent cover by forbs and an increase by grasses reported by Inouye et al. (1987).

In this report, the significance in the frequency of grasses was due, in large part, to the cool season species, smooth brome. This invading species was present 100% of the time at each transect. In contrast, the native grass species reported were located sporadically within the field. For example, the native grass big bluestem (*Andropogon gerardii* Vitman) was restricted to three contiguous clumps located in the southern region of the field on higher ground. Whereas Indian grass [*Sorghastrum nutans* (L.) Nash] was recorded along the edge of the woods on the northwest corner only. In contrast, of the most common grasses reported by Ewing (1924), only Junegrass was present in 1998 and 1999. Little bluestem and prairie dropseed were not recorded in this field.

At the north and east boundaries at the prairie-mixed hardwood oak forest interface, several forest species were recorded in the field. These included red raspberry (*Rubus strigosus* Michx.), prickly ash (*Zanthoxylum americanum* P. Mill.), box elder (*Acer negundo* L.), smooth sumac (*Rhus glabra* L.), and bur oak (*Quercus macrocarpa* Michx.). Additionally, within the field, isolated box elder and bur oak had become established, ranging in size from seedlings to mature trees. One bur oak was removed in 1999. As Gleeson and Tilman (1990) reported from the sandy soil fields of Cedar Creek Natural History Area, the fields had not become forests after 60 years. The presence of isolated trees in this field after 30 yrs appeared to follow a similar pattern.

Frequency of native forbs varied from present along each transect to species that were recorded in a single location. For example, blue-eyed grass (*Sisyrinchium angustifolium* P. Miller), was present at a single location, the lowest point in the field, and was represented by a total of five individuals both years. Slender beardtongue (*Penstemon gracilis* Nutt.) was also present at a single location but was represented by a slightly larger population of 20–25 individuals. Northern bedstraw

(*Galium boreale* L.) and sweet scented beadstraw (*Galium triflorum* Michx.) were restricted to the northwest corner, and red raspberry was restricted to the edge of the forest on the northwest.

Of the forbs observed in this study, members of the Asteraceae were recorded most frequently. However, notable for this field was the absence of indicators of healthy prairie, such as lead plant (*Amorpha canescens* Pursh) and little bluestem. Conversely, the native prairie plants that were observed were present either as long-term components or as recent invaders after 30 yrs of neglect and competition. Notwithstanding their exact origin, these species may act as indicators of microclimates within the field and serve as indicators of microclimates where related native species may also survive.

Of the native species identified, 21 were identified for inclusion in restoration projects for this field (Appendix 1). These species include representatives from thirteen floral families. Native grasses include big bluestem, Indian grass, and June grass. Native forbs include blue-eyed grass, slender beardtongue, and yarrow (*Achillea millefolium* L.).

In conclusion, although the results of this study appeared to follow a similar succession pattern compared with the results of Inouye et al. (1987) and Gleeson and Tilman (1990), the results of this study need not be over-interpreted. This study could have been improved by the use of quadrats or the canopy method described by Daubenmire (1959). These improvements will be included in subsequent studies.

Finally, the owners of this land chose not to manage the site by burning and instead were interested in a management scheme that involved a combination of selective application of herbicide and mowing. Toward this end, it is useful to know the identity of species present after thirty years. This study determined 21 native plant species growing in this field that are potentially useful for inclusion in restoration efforts at this location.

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APPENDIX 1. Plant species recorded in summer 1998 and summer 1999 in an abandoned farm field in Ottertail County, Minnesota.

Binomial	Common Name	Family	Native or Introduced	Annual or Perennial	Inclusion in Restoration
<i>Acer negundo</i> L.	boxelder	Aceraceae	N ^a	P ^c	
<i>Achillea millefolium</i> L.	yarrow	Asteraceae	N	P	yes
<i>Agropyron cristatum</i> (L.) Gaertn.	crested wheatgrass	Poaceae	I ^b	P	
<i>Agropyron repens</i> (L.) Beauv.	quackgrass	Poaceae	I	P	
<i>Agrostis stolonifera</i> L.	redtop	Poaceae	I	P	
<i>Amaranthus retroflexus</i> L.	redroot pigweed	Amranthaceae	I	A ^d	
<i>Ambrosia artemisiifolia</i> L.	common ragweed	Asteraceae	N	P	
<i>Andropogon gerardii</i> Vitman	big bluestem	Poaceae	N	P	yes
<i>Antennaria neglecta</i> Greene	field pussytoes	Asteraceae	N	P	yes
<i>Arabis glabra</i> (L.) Bernh.	tall mustard	Brassicaceae	N	B ^e	yes
<i>Artemisia frigida</i> Willd.	fringed sagewort	Asteraceae	N	P	yes
<i>Artemisia ludoviciana</i> Nutt.	white sage	Asteraceae	I	P	
<i>Asclepias syriaca</i> L.	common milkweed	Asclepiadaceae	N	P	
<i>Berteroa incana</i> (L.) DC.	hoary alyssum	Brassicaceae	I	A	
<i>Brassica kaber</i> (DC.) Wheeler	wild mustard	Brassicaceae	I	A	
<i>Bromus inermis</i> Leyss	smooth brome	Poaceae	I	P	
<i>Capsella bursa-pastoris</i> (L.) Medic.	shepherd's purse	Brassicaceae	I	A	
<i>Chenopodium album</i> L.	lamb's quarters	Chenopodiaceae	I	A	
<i>Cirsium arvense</i> L.	Canada thistle	Asteraceae	I	P	
<i>Cirsium vulgare</i> (Savi) Ten.	bull thistle	Asteraceae	I	B	
<i>Convolvulus arvensis</i> L.	field bindweed	Convolvulaceae	I	P	
<i>Conyza canadensis</i> (L.) Cronq.	horseweed	Asteraceae	N	A	
<i>Crepis capillaris</i> (L.) Wallr.	hawk'sbeard	Asteraceae	I	P	
<i>Dactylis glomerata</i> L.	orchardgrass	Poaceae	I	P	
<i>Draba nemorosa</i> L.	yellow whitlowort	Brassicaceae	N	A	yes
<i>Equisetum arvense</i> L.	field horsetail	Equisetaceae	N	P	yes
<i>Equisetum laevigatum</i> A. Br.	smooth scouring rush	Equisetaceae	N	P	yes
<i>Erigeron strigosus</i> Muhl. ex Willd.	daisy fleabane	Asteraceae	N	A	yes
<i>Fragaria virginiana</i> Duchn.	wild strawberry	Rosaceae	N	P	yes
<i>Galium boreale</i> L.	northern bedstraw	Rubiaceae	N	P	yes
<i>Galium trifolium</i> Michx.	sweet scented bedstraw	Rubiaceae	N	P	yes
<i>Hordeum jubatum</i> L.	foxtail barley	Poaceae	N	P	
<i>Koeleria pyramidata</i> (Lam.) Beauv.	Junegrass	Poaceae	N	P	yes
<i>Lathyrus venosus</i> Muhl. ex Willd.	veiny pea	Fabaceae	N	P	yes
<i>Leonurus cardiaca</i> L.	motherwort	Lamiaceae	I	P	
<i>Linaria vulgaris</i> Hill	butter and eggs	Scrophularaceae	I	P	
<i>Malva neglecta</i> Wallr.	cheeses	Malvaceae	I	A	
<i>Matricaria matricarioides</i> (Less.) Porter	pineapple weed	Asteraceae	I	A	
<i>Medicago lupulina</i> L.	black medic	Fabaceae	I	A	
<i>Medicago sativa</i> L.	alfalfa	Fabaceae	I	P	
<i>Mirabilis nycataginea</i> (Michx.) MacM.	wild 4 o'clock	Nyctaginaceae	N	P	yes
<i>Oxalis stricta</i> L.	yellow wood sorrel	Oxaladaceae	N	P	yes
<i>Parthenocissus quinquefolia</i> (L.) Planch	Virginia creeper	Vitaceae	N	P	yes
<i>Penstemon gracilis</i> Nutt.	slender beardtongue	Scrophularaceae	N	P	yes
<i>Physalis heterophylla</i> P. Mill.	clammy ground cherry	Solanaceae	N	P	yes
<i>Plantago major</i> L.	common plantain	Plantaginaceae	I	P	
<i>Poa pratensis</i> L.	bluegrass	Poaceae	I	P	
<i>Potentilla recta</i> L.	cinquefoil	Rosaceae	I	P	
<i>Quercus macrocarpa</i> Michx.	bur oak	Fagaceae	N	P	
<i>Rhus glabra</i> L.	smooth sumac	Anacardiaceae	N	P	
<i>Rubus strigosus</i> L.	red raspberry	Rosaceae	N	P	
<i>Rumex acetosella</i> L.	sheep sorrel	Polygonaceae	I	P	
<i>Rumex crispus</i> L.	curly dock	Polygonaceae	I	P	
<i>Setaria viridis</i> (L.) Beauv.	green foxtail	Poaceae	I	A	
<i>Silene noctiflora</i> L.	night flowering catchfly	Caryophyllaceae	I	A	
<i>Silene pratensis</i> (Raf.) Godr. & Gren.	white campion	Caryophyllaceae	I	P	
<i>Sisyrinchium angustifolium</i> P. Miller	blue eyed grass	Iridaceae	N	P	yes
<i>Solidago missouriensis</i> Nutt.	Missouri goldenrod	Asteraceae	N	P	yes

APPENDIX 1. Continued.

Binomial	Common Name	Family	Native or Introduced	Annual or Perennial	Inclusion in Restoration
<i>Solidago rigida</i> L.	rigid goldenrod	Asteraceae	N	P	yes
<i>Sonchus arvensis</i> L.	sow thistle	Asteraceae	I	P	
<i>Sorghastrum nutans</i> (L.) Nash	Indian grass	Poaceae	N	P	yes
<i>Taraxacum officinale</i> L.	dandelion	Asteraceae	I	P	
<i>Toxicodendron radicans</i> (L.) O. Ktze.	poison ivy	Anacardiaceae	N	P	
<i>Tradescantia bracteata</i> Small	bracted spiderwort	Commelinaceae	N	P	yes
<i>Tragopodon dubius</i> Scop.	goatsbeard	Asteraceae	I	P	
<i>Trifolium hybridum</i> L.	aslike clover	Fabaceae	I	P	
<i>Urtica dioica</i> L.	stinging nettle	Urticaceae	N	P	
<i>Verbascum thapsus</i> L.	common mullein	Scrophularaceae	I	B	
<i>Vicia sativa</i> L.	common vetch	Fabaceae	I	P	
<i>Zanthoxylum americanum</i> P. Mill.	prickly ash	Rutaceae	N	P	

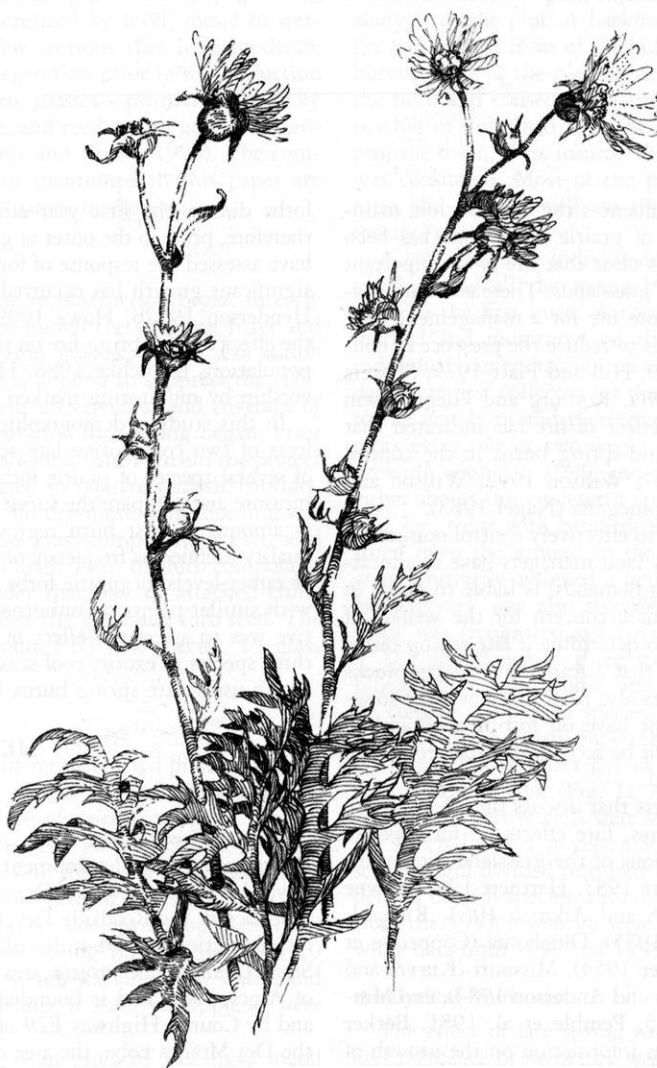
^aNative species recorded in the field

^bIntroduced species recorded in the field

^cPerennial species recorded in the field

^dAnnual species recorded in the field

^eBiennial species recorded in the field



Effects of Late Spring Fires on the Survival, Growth, and Reproduction of Prairie Forbs

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In May of 1998 and 1999, late spring fires were conducted on 2×5 m plots on a prairie reconstruction in central Iowa. Prior to the 1998 burn, 195 individual plants of 21 forb species were marked on the spring burn plots and on adjacent control plots. Over the next two years, and following a second burn in 1999, these marked plants were monitored to assess survivorship, reproduction, and incidence of herbivory. The tiller density of three non-native, cool-season grasses was measured on the control and spring burn plots in 1997 prior to the first burn and at the end of the growing season in 1998 and 1999. No difference in survivorship within the forb community was observed between control and spring burn at anytime in the study, although one species—common wormwood—exhibited significantly lower survivorship on the burn plots. Flower production was significantly lower for forb species in the burn plots than the control plots in both years, and herbivory was significantly higher for forb species in the burn plots than the control plots in 1998 (no difference in 1999). It was apparent that herbivory contributed to lower flower production. Per capita growth of smooth brome tillers was significantly lower on burn plots for both 1998 and 1999. These results indicate that late spring fires can be used as an effective tool to combat non-native species in prairies without causing detrimental effects to the integrity of the forb community.

INDEX DESCRIPTORS: late spring fire, forbs, survival, flowering, demography, herbivory, exotic cool-season grasses.

The myriad ways in which fire influences the composition, maintenance, productivity and function of prairie ecosystems has been well-studied for several decades. It is clear that fire is an important and natural environmental feature of grasslands. There are many reasons why land managers might choose fire for a management tool; among the most prominent of these is to reduce the presence of non-native, cool-season grasses (Old 1969, Hill and Platt 1975, Masters et al. 1992, Engle and Bultsma 1984, Rosburg and Glenn-Lewin 1992). Research investigating this effect of fire has indicated that late spring burns surpass early or mid-spring burns in the control of smooth brome (Blankespoor 1987, Willson 1992, Willson and Stubbendieck 1997) and Kentucky bluegrass (Nagel 1983).

The need to use late spring burns to effectively control non-native grasses, combined with the difficulty land managers have in allocating time for all their spring burning demands, is liable to result in late spring burns that cause legitimate concern for the welfare of prairie forbs. Thus, it is important to determine if late spring burns kill or otherwise stress prairie forbs that already have several weeks of growth underway. Prairie managers also need to know what long-term effects late spring burns might have on forb species and to what extent those consequences might be acceptable if better control of non-native species can be achieved.

The literature is replete with papers that discuss the effects of fire on the species composition of prairies. Fire effects on forb species have been documented in many regions of the grassland biome, including Kansas (Abrams and Hulbert 1987, Hartnett 1991, Towne and Knapp 1996), Iowa (Ehrenreich and Aikman 1963, Richards and Landers 1973, Hill and Platt 1975), Oklahoma (Coppedge et al. 1998), Wisconsin (Dix and Butler 1954), Missouri (Kucera and Koelling 1964), Illinois (Schwegman and Anderson 1984), and Minnesota (Svedarsky and Buckley 1975, Pemble et al. 1981, Becker 1989). Most of this research provides information on the growth of

forbs during the first year after an early or mid-spring fire, and therefore, prior to the onset of growth for most species. Fewer studies have assessed the response of forbs to late spring fires that occur after significant growth has occurred (Lovell et al. 1983, Leoschke 1986, Henderson 1992b, Howe 1999). Even fewer studies have assessed the effect of late spring fire on reproductive variables in specific plant populations (Leoschke 1986, Henderson 1992a) or measured survivorship by monitoring marked individuals.

In this study, a demographic approach was used to assess the effects of two consecutive late spring burns on the vigor and health of several species of prairie forbs. Specifically, the objectives were to measure and compare the survival rates, the amount of vigor (defined as amount of post burn regrowth), and the levels of reproductive quality (defined as frequency of flower production at either the genet or ramet levels) of prairie forbs on plots burned in early to mid May with similar plants on unburned control plots. An additional objective was to assess the effect of late spring burns on the density of three species of exotic, cool-season grasses in order to assess the benefit in using late spring burns for prairie management.

METHODS

Study Site

The study was a part of a larger, long-term project that is currently investigating the development of reconstructed prairie in central Iowa. In 1996, the Iowa Department of Transportation, under the guidance of the Roadside Development Section, completed a prairie reconstruction on $4\frac{1}{2}$ miles of right-of-way along Interstate 35 in Story County. The project area is located along the eastern margin of Ames, Iowa, and is bounded by U.S. Highway 30 on the south and by County Highway E29 on the north. Story County lies within the Des Moines Lobe, the area of the state that was glaciated during

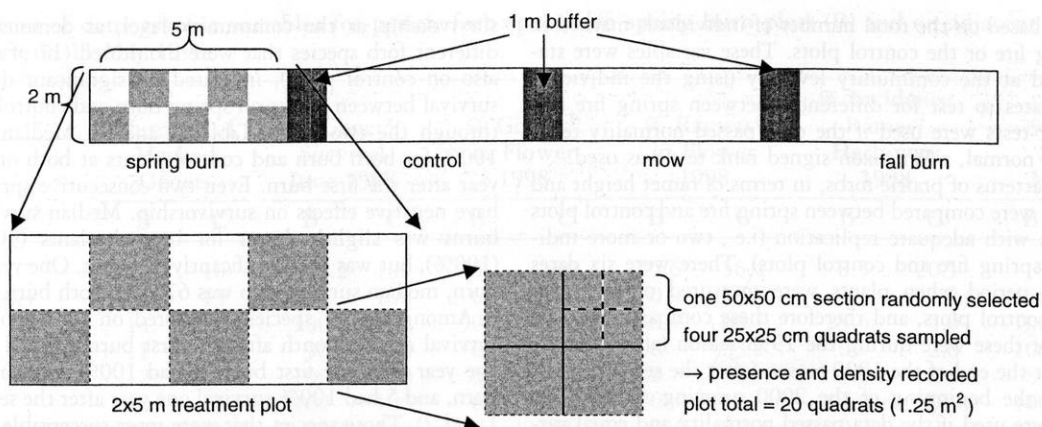


Fig. 1. Experimental design and sampling methodology for study sites on the Interstate 35 prairie reconstruction. For the purposes of this paper, only the spring fire and control plots are utilized.

the late stages of the Wisconsinan glaciation between 14,000 and 12,000 years ago. Therefore, the landscape is generally level and poorly drained. Story County has a continental climate representative of the temperate grassland biome.

Most of the project area is characterized by level, mesic to wet-mesic soils, although there are a few sections that have moderate slopes and well-drained soils. The vegetation prior to reconstruction was dominated by cool-season, exotic grasses—primarily Kentucky bluegrass, smooth brome, tall fescue, and reed canary grass. Nomenclature for plant species follows Eilers and Roosa (1994). The common names of all species studied or mentioned in this paper are cross-referenced with their scientific names in Appendix A.

Prairie Reconstruction History

Preparation of the seedbed for the reconstruction began in early April by mowing the project area to mulch the standing litter and hasten the early growth of cool-season grasses. When cool-season growth was underway, glyphosate was applied to suppress the cool-season grasses. By mid-May, when the effectiveness and coverage of the application was confirmed, preparation for seeding began. Prior to seeding, 15 study sites (Fig. 1) were established within the project area. Eleven of these sites were located in relatively mesic habitats, while the other five were established in dry-mesic soils. Seeding was accomplished in two stages. First, the grass component of each seed mix was drilled with a Truax no-till drill. Then the forb component was seeded with a Buffalo dropseeder that had an attached cultipacker that pressed the soil down over the grass and forb seed. The seed mix used on the 15 sites contained 65 forb species, 13 grass species, and 5 shrub species.

Field Methods

The community composition of the reconstructed prairie has been monitored on each of the 15 study sites at the end of the growing season every year since 1996. Each study site consists of a block represented by four 2×5 m treatment plots—control, fall fire, spring fire, and summer mow (Fig. 1). In the fall of 1997 and spring of 1998, burning treatments were initiated at the study sites and were applied for two consecutive years. The spring burn in 1998 occurred on May 11, and the second spring burn occurred on 10 May 1999. In both years the spring season was unusually warm, and growth by prairie forbs was very obvious; in some cases, plants were between 15 and 30 cm in height.

Burns were confined to the 2×5 m plots by placing a metal

panel on the boundary with the adjacent plot, mowing and raking a fire lane along the other three sides of the plot, and wetting the perimeter heavily with water. The fire lanes were located about 2 m from the treatment plot. In that way, 2 m of buffer strip were burned along with the plot. A backfire was used to start the fire. Once the fire had burned most of the buffer strip, a headfire was started which burned most of the plot. In order to minimize the heterogeneity in the burn and consequently the experimental error in the study, any patches of unburned litter or area were ignited and burned with a propane torch. This insured that at least 90% of the litter on a plot was consumed. Most of the plots had a high litter/green biomass ratio and burned well, so the torch was necessary in only a few instances each year.

A cohort of 120 individuals representing 21 forb species was located among all the spring burn plots and marked in May 1998 prior to the first burn. A comparable group of 75 individuals was marked and monitored on the control plots. Ramet number and individual ramet heights were recorded for each individual. These data were first collected for the plants on the spring burn plots prior to the first burn and thereafter for plants on both burn and control plots every one or two weeks during 1998, once at the end of the growing season in 1999, and once during spring 2000. Ramets are either shoots (for caulescent species) or caudices (for acaulescent species, i.e., those with basal leaves). Ramet height for shoots was measured from the ground to the highest node on the stem. Caudices were arbitrarily assigned a height of 1 cm. Occurrence of flowering or herbivory was also recorded for each ramet. Herbivory in this study was recognized as a cut stem, presumably caused by rabbits.

The abundance of three species of cool-season grass (Kentucky bluegrass, smooth brome, and tall fescue) was monitored each year by completing annual species inventories of the treatment plots in late August and early September. A stratified random sampling design was used to select five of the ten 1×1 m cells within a 2×5 m treatment plot (Fig. 1). After selecting the first 1×1 cell at random, successive cells were selected in an alternate pattern. Within the selected 1×1 m cell, a 50×50 cm sample plot was randomly selected and divided into four quadrats each 25×25 cm. The tiller density of each species was tabulated for each of these quadrats. Data from the 1997 inventory were used as a baseline pretreatment level, while data from 1998 and 1999 were used as response measurements.

Analytical Methods

The effect of late spring fire on survivorship, flower production, and incidence of herbivory was assessed for each species by calculat-

ing proportions based on the total number of individuals marked in either the spring fire or the control plots. These variables were statistically assessed at the community level by using the individual species as replicates to test for differences between spring fire and control. Paired t-tests were used if the data passed normality tests. If data were not normal, a Wilcoxon signed rank test was used.

The growth patterns of prairie forbs, in terms of ramet height and ramet frequency, were compared between spring fire and control plots for those species with adequate replication (i.e., two or more individuals in both spring fire and control plots). There were six dates over a two-year period when plants were measured on both the spring fire and control plots, and therefore these comparisons could be made. Four of these were during the 1998 season (after the first burn), one was at the end of the 1999 season (after the second burn), and one was at the beginning of the 2000 growing season. Two sample t-tests were used if the data passed normality and equal variance tests. If either of these failed, a Mann-Whitney rank sum test was used. Replication was provided by the marked individuals and therefore was reduced during the course of the two-year period if mortality occurred. There were 11 species with adequate replication at the start of the study.

The responses of the cool-season grasses to the late spring burns were analyzed by calculating species per capita growth rates between a given initial year and a subsequent response year. The per capita growth rate (r) is the number of tillers added to or lost from the population per individual tiller in the population.

$$r = \frac{\ln\left(\frac{\text{response year density} + 1}{\text{initial year density} + 1}\right)}{\text{time (response year} - \text{initial year)}}$$

A value of 1 was added to density measurements to allow calculation when density was 0. Positive values of (r) indicate an increasing population; negative values indicate a decreasing population. Per capita growth rates (r) were determined for the effect of the first spring burn (1997 to 1998), for the effect of the second spring burn (1998 to 1999), and for the combined effect of both spring burns (1997 to 1999). In this way it can be determined whether a species response occurred primarily in just one of the years or if it was a cumulative effect over the course of the consecutive treatments. An effect observed in 1997 to 1998 might either be maintained (still present in 1997 to 1999), reversed (absent in 1997 to 1999), or enhanced (repeated effect in 1998 to 1999).

The values of (r) for each species were analyzed with analysis of variance (ANOVA) using the following model. Potential sources of variation in (r) were: 1) treatments (comparison between spring fire and control), 2) seed mix (which represents different environmental conditions—dry-mesic vs. mesic sites), and 3) site within seed mix (which represents variation due to differences in site characteristics such as biotic or historical factors). Parametric ANOVA was used on JMP software by Statistical Analysis Systems, Inc.

Replication in this study was provided by the 15 sites. In order for a site to be included as a replicate, it was necessary for the species to have a valid presence on the site. This was arbitrarily defined as having at least 33% nonzero observations among the six potential observations (2 treatment plots over 3 years equals 6 observations, thus 2 or more nonzero observations on the site were necessary to be included as a replicate). Replication for the analyses of treatment effects on the cool-season grasses ranged from 11 to 15.

RESULTS

Demography of Forbs

Observations one week after the fires verified that all the marked plants on the spring burn plots were topkilled by the fires. Forb

survivorship at the community level, as demonstrated by the 21 different forb species that were monitored (17 of these species were also on control plots), indicated no significant difference in genet survival between plants on spring burn and control plots at any time through the two years (Tables 1 and 2). Median survivorship was 100% for both burn and control plants at both one month and one year after the first burn. Even two consecutive spring burns did not have negative effects on survivorship. Median survivorship after two burns was slightly lower for burned plants (90%) than control (100%), but was not significantly different. One year after the second burn, median survivorship was 67% for both burn and control plots.

Among the 21 species monitored on burn plots, 17 had 100% survival at one month after the first burn, 16 had 100% survival at one year after the first burn, 9 had 100% survival after the second burn, and 5 had 100% survival one year after the second burn (Tables 1 and 2). Those species that were most susceptible to late spring fire were common wormwood, New England aster, and western ironweed. These species had burn survivorship values that were at least 10% lower than the control by May 2000. Since common wormwood is a non-native, accidental species in the reconstruction, reduction of it is a beneficial result for the reconstruction.

Overall reproductive quality among the 21 species was lower for plants on the spring burn plots compared to plants on the control plots during the growing seasons following both the first and second burn (Tables 1 and 2). Both the percentage of genets in flower and the percentage of ramets in flower for burn plants was significantly lower than for control plants after the first burn. There was less difference in reproductive quality during the 1999 growing season after the second burn (Table 2). Although the percentage of ramets in flower was still significantly greater for control plants than for spring fire, the percentage of genets in flower was not significantly different.

Although the reproductive quality of the prairie forb community was measurably reduced by late spring fire, the numbers of species that were intolerant to the fire compared to those demonstrating tolerance of fire was fairly similar (Table 3). With respect to a species ability to cope with the stresses of topkilling by a late spring fire and its subsequent reproduction, wild bergamot, common wormwood, and purple prairie clover were among the most consistently intolerant to late spring fire (no flowering on burn plots while control plants flowered). Those species that demonstrated consistent tolerance to late spring fire (flowering occurred in plants on both plots) included black-eyed susan, ox-eye, and Canada milkvetch.

Herbivory in the prairie forb community was significantly higher (about 500%) on plants in the burn plots than the control plots during the 1998 growing season following the first spring burn (Table 1). About 50% of the species on the burn plots exhibited evidence of herbivory, while less than 25% of the same species were grazed on control plots. This pattern did not occur in the 1999 growing season after the second burn. There was no significant difference in the percentage incidence of ramet herbivory in 1999, although herbivory was slightly higher in the spring fire plots compared to the control plots (Table 2). There was also no difference in early season herbivory (in May 2000 one year after the second burn) between spring fire and control plots, although median percentage incidence of herbivory was slightly higher on control plots (Table 2).

Although a significant difference in herbivory at the community level was only observed in 1998, species-specific differences were apparent each year (Table 4). The species consistently selected with greater frequency on the burn plots were the asters, including azure aster, smooth aster, and New England aster. Ox-eye plants on the burn plots were also selected by the herbivores in 1999 more often than plants on the control plots. A similar number of species were avoided on the burn plots and grazed with higher frequency on the

Table 1. Comparison of demographic variables for prairie forb species on spring burn plots (B) and on adjacent control plots (C) following a burn on 11 May 1998.

Species	Number of Marked Genets		% Genet ^a Survival June 1998		% Genets ^b in Flower 1998		% Ramets ^c in Flower 1998		% Incidence Ramet ^d Herbivory 1998		% Genet ^e Survival May 1999	
	B	C	B	C	B	C	B	C	B	C	B	C
black-eyed susan	21	10	95.2	100	75	80	55.6	56.4	8.5	20.5	9.5	0
grey headed coneflower	15	13	100	100	0	53.8	0	13.6	0	1.7	100	100
ox-eye	14	10	100	100	50	90	8.7	66.7	23.6	5.0	100	100
wild bergamot	11	6	90.9	100	0	50	0	23.1	0	2.6	100	83.3
frost aster	12	4	100	100	0	0	0	0	7.1	0	83.3	75.0
New England aster	10	5	100	100	0	0	0	0	34.0	0	100	100
common wormwood	7	5	71.4	100	0	80	0	34.1	0	0	28.6	100
Canada milkvetch	6	3	100	100	66.7	100	30.0	58.3	2.9	0	83.3	33.3
smooth aster	5	3	100	100	0	0	0	0	45.3	0	100	100
sweet coneflower	3	2	66.7	100	0	0	0	0	0	0	100	100
azure aster	2	2	100	100	0	0	0	0	46.2	0	100	100
Canada goldenrod	1	3	100	100	0	0	0	0	0	0	100	100
giant goldenrod	3	1	100	100	66.7	100	44.4	100	11.1	0	100	100
rigid goldenrod	1	3	100	100	0	0	0	0	0	0	100	100
golden alexander	3	0	100	—	0	—	0	—	100	—	100	—
prairie fleabane	1	2	100	100	0	100	0	100	0	0	0	0
purple prairie clover	1	2	100	100	0	100	0	100	11.1	0	100	100
western ironweed	1	1	100	100	0	0	0	0	0	0	100	100
rosin weed	1	0	100	—	0	—	0	—	0	—	100	—
round headed bush clover	1	0	100	—	100	—	42.9	—	0	—	100	—
thimble weed	1	0	100	—	0	—	0	—	0	—	100	—
Totals	120	75										
Means*/Medians			100	100	0	50.0	0	13.6	11.2*	1.8*	100	100
Probability ^f			0.13		0.004		0.004		0.037		0.63	

^athe proportion of marked genets that were alive one month after the spring burn (alive 10 June 1998)

^bthe proportion of those genets that survived the burn that produced at least one flower by the end of July 1998

^cthe proportion of ramets present that produced at least one flower by the end of July 1998

^dthe proportion of ramets present that exhibited evidence of herbivory by the end of July 1998

^ethe proportion of marked genets that survived the burn and following winter (alive 10 May 1999)

^fP-values for either paired t-tests (means) or signed rank test (medians)

control plots (Table 4). This was most evident when herbivory was assessed in late spring. Herbivores selected similar species in late spring as they did later in the growing season, but general differences in seasonal usage was evident in that grey-headed coneflower, sweet coneflower, Canada goldenrod, and rigid goldenrod were grazed more frequently in the spring than late summer (compare May 2000 vs. August 1999), and ox-eye, New England aster, and azure aster were grazed more frequently in late summer than in the spring (Table 2).

Species Specific Growth Responses to Late Spring Fire

The 11 species that were replicated in both burn and control plots were analyzed in more detail by comparing their growth between burn and control plots at six times during the study. The most consistent pattern was a decrease in ramet height in the plants on the spring burn plots relative to the control plots during the growing season after the first late spring burn. Ten of the 11 species (Table 5) exhibited significantly lower ramet height on at least one date and more often on three or four dates (Fig. 2–4). During 1998, the average height of ramets of plants stressed by the spring burn was typically only 50% (sometimes as low as 25%) of the height of ramets on unburned controls. For strongly basal-leaved species like

grey-headed coneflower and common wormwood, ramet height of spring burn plants was as little as 5% or less of the ramet height of control plants. For 9 of these 10 species, the burned plants did not recover enough growth by the end of July 1998 for the average ramet height to equal the control plants. In general, plants that experienced a second late spring burn had ramet heights at the end of the 1999 growing season that were also significantly lower than on counterparts in control plots (Table 5, Fig. 2). In the eight species with sufficient replication to allow statistical comparison in August 1999, five exhibited significantly greater ramet height in the control than in the spring fire plots (Table 5). In another two species, the height of ramets in control plots tended to be higher than ramets in spring fire plots. In the seven species that could be statistically tested one year after the second burn (May 2000), only one species (wild bergamot) exhibited a significant difference in ramet height (Table 5). In all the other species, the plants had either recovered from the consecutive burns by this time, or perhaps more likely, there had not been enough growing season time for differences to develop.

Ramet frequency was more variable than ramet height in terms of its response to the late spring burn. There were three basic patterns observed among the 11 species that basically define three over-

Table 2. Comparison of demographic variables for prairie forb species on spring burn plots (B) and on adjacent control plots (C) after two consecutive spring burns on 11 May 1998 and 10 May 1999. If no plants remained, (np) indicates no calculation was possible.

Species	Number of Marked Genets		% Genet ^a Survival May 1999		% Genet ^b Survival Aug. 1999		% Genet ^c in Flower 1999		% Ramets ^d in Flower 1999		% Incidence Ramet ^e Herbivory 1999		% Genet ^f Survival May 2000		% Incidence Ramet ^g Herbivory May 2000	
	B	C	B	C	B	C	B	C	B	C	B	C	B	C	B	C
black-eyed susan	21	10	9.5	0	4.8	0	100	np	100	np	0	np	4.8	0	0	np
grey headed coneflower	15	13	100	100	100	92.3	53.3	75.0	31.0	41.2	1.8	8.2	93.3	92.3	36.1	50.3
ox-eye	14	10	100	100	92.9	100	69.2	90.0	19.8	72.0	43.4	21.5	85.7	80.0	8.4	13.6
wild bergamot	11	6	100	83.3	90.9	83.3	0	100	0	78.3	11.6	0	90.9	83.3	3.0	7.5
frost aster	12	4	83.3	75.0	41.7	75.0	0	66.7	0	36.4	16.7	0	66.7	75.0	0.6	22.2
New England aster	10	5	100	100	90.0	100	33.3	80.0	8.6	54.8	37.9	16.1	80.0	100	22.8	4.3
common wormwood	7	5	28.6	100	0	100	np	80.0	np	41.4	np	5.2	0	100	np	0
Canada milkvetch	6	3	83.3	33.3	66.7	33.3	75.0	0	33.3	0	0	100	50.0	0	0	np
smooth aster	5	3	100	100	80.0	100	0	66.7	0	50.0	65.2	12.5	80.0	66.7	25.0	33.3
sweet coneflower	3	2	100	100	100	100	0	100	0	100	6.3	0	100	100	8.7	37.9
azure aster	2	2	100	100	100	100	100	50.0	64.7	83.3	52.9	8.3	50.0	50.0	0	0
Canada goldenrod	1	3	100	100	100	100	0	66.7	0	90.5	15.4	4.8	100	66.7	40.9	17.2
giant goldenrod	3	1	100	100	66.7	100	0	0	0	0	10.0	50.0	33.3	0	0	np
rigid goldenrod	1	3	100	100	100	100	100	66.7	100	62.5	0	0	100	100	0	22.2
golden alexander	3	0	100	—	100	—	0	—	0	—	0	—	66.7	—	33.3	—
prairie fleabane	1	2	0	0	0	0	np	np	np	np	np	np	0	0	np	np
purple prairie clover	1	2	100	100	0	50.0	np	100	np	100	np	0	0	0	np	np
western ironweed	1	1	100	100	100	100	100	100	37.5	100	12.5	0	0	100	np	0
rosin weed	1	0	100	—	100	—	100	—	16.7	—	0	—	100	—	0	—
round headed bush clover	1	0	100	—	0	—	np	—	np	—	np	—	0	—	np	—
thimble weed	1	0	100	—	100	—	0	—	0	—	0	—	100	—	0	—
Totals	120	75														
Means*/Median			100	100	90	100	40.8*	66.3*	22.7*	59.2*	21.1*	17.0*	66.7	66.7	14.6	20.9
Probability ^h			0.63		0.18		0.13		0.01		0.71		1.0		0.27	

^athe proportion of marked genets that survived the first burn and winter (alive 10 May 1999 at time of second burn)

^bthe proportion of marked genets that survived burn 1, winter 98–99, and burn 2 (alive 20 August 1999)

^cthe proportion of those genets that survived the burns and produced at least one flower by the end of August 1999

^dthe proportion of ramets present that produced at least one flower by the end of August 1999

^ethe proportion of ramets present that exhibited evidence of herbivory by the end of August 1999

^fthe proportion of marked genets that survived burn 1, winter 98–99, burn 2, and winter 99–00 (alive 20 May 2000)

^gthe proportion of ramets present that exhibited evidence of herbivory in May 2000

^hP-values for either paired t-tests (means) or signed rank test (medians)

Table 3. Patterns of reproduction among forbs on spring burn and control plots.

Species Patterns After One Burn (in 1998)		Species Patterns After Two Burns (in 1999)	
Flowering on Control But Not on Burn (Intolerant Species)	Flowering on Both Control and Burn (Tolerant Species)	Flowering on Control But Not on Burn (Intolerant Species)	Flowering on Both Control and Burn (Tolerant Species)
grey-headed coneflower	black-eye susan	wild bergamot	black-eye susan ^a
wild bergamot	ox-eye	common wormwood	grey-headed coneflower
common wormwood	Canada milkvetch	frost aster	ox-eye
prairie fleabane	giant goldenrod	smooth aster	Canada milkvetch ^a
purple prairie clover		sweet coneflower	New England aster
		Canada goldenrod	azure aster
		purple prairie clover	rigid goldenrod
			western ironweed

^aflowering plants were only observed on the burn plots

Table 4. Patterns of herbivory among forbs on spring burn and control plots. Species are grouped according to the magnitude of the difference in % incidence herbivory between spring burn and control plots. Numbers in () refer to the measurement time—1 represents mid-summer 1998, 2 represents late summer 1999, and 3 represents spring 2000.

(% Incidence of Ramet Herbivory in Spring Burn Plots – % Incidence of Ramet Herbivory in Control Plots)		
Difference ≥ 20% (Strong Preference for Burn)	–20% < Difference < 20% (More or Less Equal Preference)	Difference ≤ –20% (Strong Preference for Control)
azure aster (1,2)	azure aster (3)	Canada milkvetch (2)
Canada goldenrod (3)	black-eyed susan (1)	frost aster (3)
New England aster (1,2)	Canada goldenrod (1,2)	giant goldenrod (2)
ox-eye (2)	Canada milkvetch (1)	rigid goldenrod (3)
smooth aster (1,2)	common wormwood (1)	sweet coneflower (3)
	frost aster (1,2)	
	giant goldenrod (1)	
	grey-headed coneflower (1,2,3)	
	New England aster (3)	
	ox-eye (1,3)	
	prairie fleabane (1)	
	purple prairie clover (1)	
	rigid goldenrod (1,2)	
	smooth aster (3)	
	sweet coneflower (1,2)	
	western ironweed (1,2)	
	wild bergamot (1,2,3)	

all response types to a late spring burn. In some cases, ramet frequency was greater on spring burn plots than on control plots (Fig. 2). This was demonstrated most significantly by ox-eye and frost aster and to a lesser degree by smooth aster, New England aster, and Canada milkvetch. The second type of response was no significant difference in ramet frequency between spring fire and control (Fig. 3). In these five species (sweet coneflower, grey-headed coneflower, azure aster, black-eyed susan, and wild bergamot), differences in ramet frequency between the two treatments through the 1998 growing season were generally less than two or three ramets. The third type of response was a significant decrease in ramet frequency on the spring fire plots compared to the control plots. Only one species, common wormwood, exhibited this response (Fig. 4).

Effects of Late Spring Fire on Exotic, Cool-season Grasses

Late spring fires in both 1998 and 1999 caused significant reduction in the tiller density of smooth brome (Fig. 5). Significance was

greatest in the 1998 to 1999 comparison (first year response after the second burn). Tiller density of tall fescue and Kentucky bluegrass increased consistently and similarly between 1997 and 1999 on both burn and control plots. However, no significant differences occurred in per capita population growth between control and spring burn plots for any of the year comparisons in either species (Fig. 5).

DISCUSSION

None of the native prairie forbs monitored exhibited any evidence that topkilling by one late spring fire resulted in mortality or in stress that compromised their ability to survive the winter season. In fact, for at least two species, survivorship one year after the first burn was a little higher on burn plots than on control plots. Even two years of consecutive late spring burns did not have adverse effects on the survival of the native forb community. These results were obtained in a reconstruction where the plants were no older than two years at the time of the first burn. It seems logical to expect

Table 5. Patterns among species growth responses on spring burn and control plots. See figures 2–4 for dates of measurements. Use of either \ll or \gg indicates a significant difference ($P < 0.10$) in ramet height or frequency between spring burn (B) and control (C) plots. A single $<$ or $>$ indicates a non-significant trend in the difference, and NR indicates “no replication,” therefore, no comparison could be made.

Species	Replicates (in 5/98)	Mean Ramet Height			Mean Ramet Frequency			Overall Response Type
		1998	1999	2000	1998	1999	2000	
ox-eye	14–10	B \ll C	B \ll C	B = C	B \gg C	B = C	B = C	compensatory
frost aster	12–4	B \ll C	B \ll C	B = C	B \gg C	B = C	B $>$ C	compensatory
Canada milkvetch	6–3	B \ll C	NR	NR	B $>$ C	NR	NR	compensatory ?
New England aster	10–5	B \ll C	B \ll C	B = C	B $>$ C	B = C	B = C	compensatory ?
smooth aster	5–3	B \ll C	B $<$ C	B = C	B $>$ C	B $>$ C	B $>$ C	compensatory ?
sweet coneflower	3–2	B \ll C	B \ll C	B = C	B = C	B = C	B $<$ C	intolerant
grey-headed coneflower	15–13	B \ll C	B $<$ C	B = C	B = C	B $>$ C	B = C	intolerant
azure aster	2–2	B $<$ C	B = C	NR	B = C	B = C	NR	intolerant
black-eyed susan	21–10	B \ll C	NR	NR	B = C	NR	NR	intolerant
wild bergamot	11–6	B \ll C	B \ll C	B \ll C	B = C	B = C	B = C	intolerant
common wormwood	7–5	B \ll C	NR	NR	B \ll C	NR	NR	very intolerant

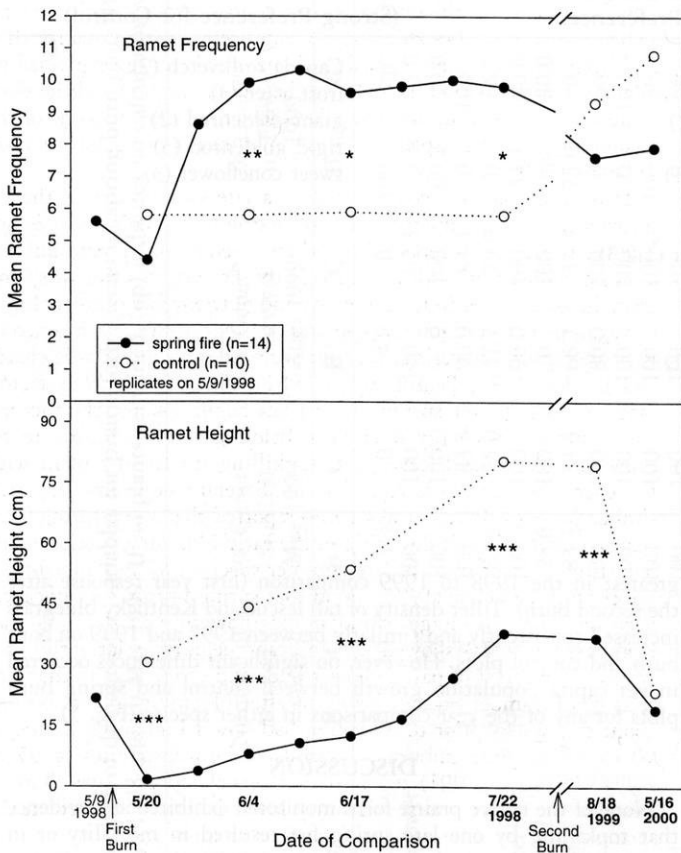


Fig. 2. Ramet frequency and height of ox-eye on spring fire and control plots. Consecutive burns were conducted on 11 May 1998 and 10 May 1999. Two sample statistics were used to compare ramet height and frequency on six different dates. Significant differences between control and fire means/medians within date are indicated for various levels by * ($P < 0.10$), ** ($P < 0.05$), and *** ($P < 0.005$). Insufficient replicates for a test is indicated with (nr).

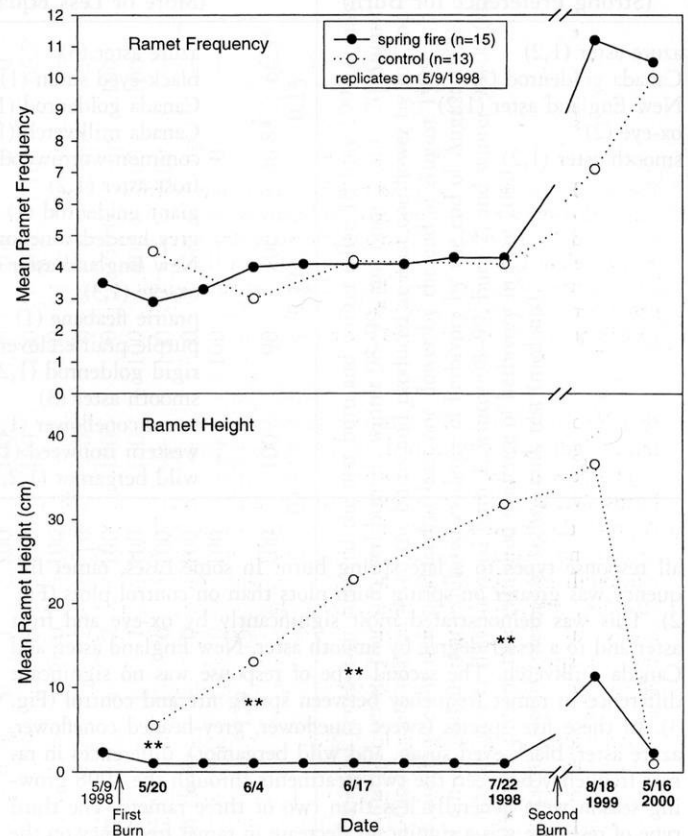


Fig. 3. Ramet frequency and height of grey-headed coneflower on spring fire and control plots. Consecutive burns were conducted on 11 May 1998 and 10 May 1999. Two sample statistics were used to compare ramet height and frequency on six different dates. Significant differences between control and fire means/medians within date are indicated for various levels by * ($P < 0.10$), ** ($P < 0.05$), and *** ($P < 0.005$). Insufficient replicates for a test is indicated with (nr).

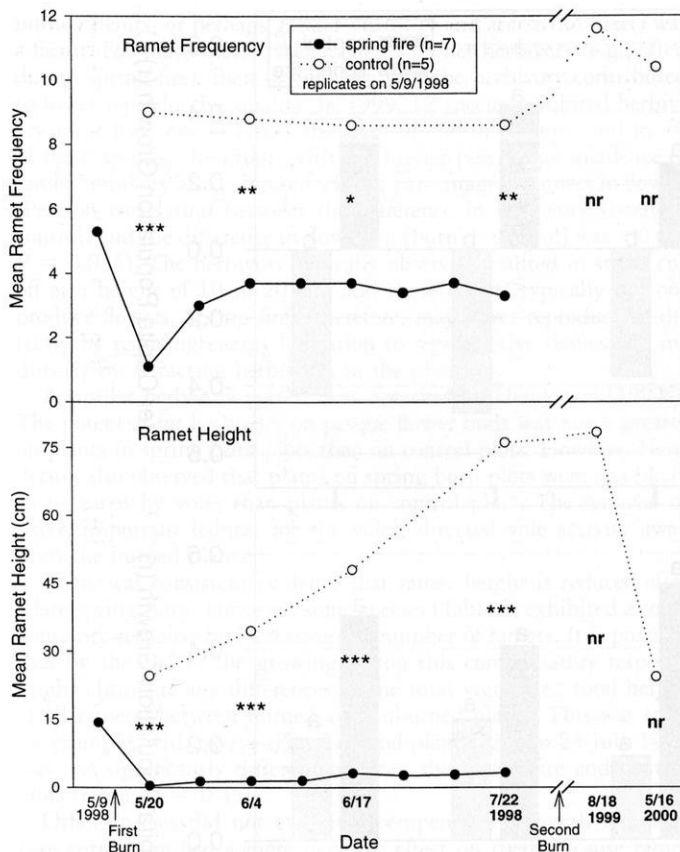


Fig. 4. Ramet frequency and height of common wormwood on spring fire and control plots. Consecutive burns were conducted on 11 May 1998 and 10 May 1999. Two sample statistics were used to compare ramet height and frequency on six different dates. Significant differences between control and fire means/medians within date are indicated for various levels by * ($P < 0.10$), ** ($P < 0.05$), and *** ($P < 0.005$). Insufficient replicates for a test is indicated with (nr).

that forb mortality in a remnant prairie where plants are older and more vigorously established would be even less likely.

Henderson (1992b) reported on the effect of eight late spring burns over a ten-year period on a dry-mesic prairie in Wisconsin. Among the eight species of native forbs measured, five species exhibited no change, two species decreased, and one species increased. Although individual survival data were not obtained by Henderson (1992b), the results combined with the longevity of the study certainly suggested that individuals of several species were surviving the late spring burns. Many prairie forbs appear to be very capable of surviving the stress associated with topkilling by a late spring fire.

An exception may be golden alexander. In another study in Wisconsin, Howe (1999) recorded a decrease in density ($\approx 50\%$) of golden alexander after a late spring burn (although the decrease was only half the per capita rate observed on the control). In the present study, however, golden alexander exhibited tolerance of late spring fire. The three golden alexander plants marked on spring burn plots all survived the first fire, and two of the three were alive in May 2000 one year after the second fire. There were no golden alexander on the control plots to use for comparison, but none are needed to verify survival (controls would confirm if mortality on burn plots was caused by the fire).

The mortality incurred by common wormwood appears to be related to a combined effect of the burn and the stress associated with winter. Survivorship for common wormwood at one year after the first burn (29%) was much lower than at one month after the first burn (71%) (Table 1). Likewise, the mortality observed for some of the individuals of New England aster and western ironweed on the burn plots (the two native species indicated as more susceptible to late spring burns) did not occur right after the second burn, but rather during the winter following the second burn. Thus, the combined effect of fire and winter is also indicated in the mortality of individuals in these two species. This synergistic effect occurred despite the fact that the two winter seasons involved (97–98 and 98–99) were warmer than normal. Because the stress of winter appears to be important for some species, it is possible that long-term mortality could be higher after late spring burns if the plants experience greater stress associated with normal or below normal winter temperatures.

As a whole, reproductive quality was artificially low on both the burn and control plots for 1998 because the plants were not monitored through the entire growing season (just to the end of July). The low reproductive quality on the control plots (50% for genets and 14% for ramets in 1998) may be due to the lack of observations after August or to their young age (less than 3 yrs into the reconstruction). Because most of the species in this category were asters and goldenrods (Table 1), the effect of sampling time is a good possibility. Despite the setback of two consecutive late spring burns, prairie forbs in 1999 exhibited a greater reproductive quality than had been observed the year before. Some of this can be explained by a later sampling period in 1999 (to the end of August) and therefore a greater likelihood of observing late-flowering species. Some of the change may also be explained by the maturation of the plants from 1998 to 1999.

It is clear that one consequence of a late spring burn is the reduction in the reproductive vigor of prairie forbs. This result is unlike the observations reported by others when assessing reproduction after an early or mid-spring burn. If the fire occurs prior to spring growth, the changes in microclimate and nutrient flux promote higher vegetative production (Knapp and Seastedt 1986) and a concomitant increase in flowering, even for spring flowering forbs (Richards and Landers 1973, Pemble et al. 1981). Timing is the key factor; fires that occur after spring growth has begun change the picture. The depletion of energy reserves in below ground structures to regrow new shoots and leaves after topkilling results in a plant with less energy to allocate to reproduction. Several studies have reported similar patterns. Lovell et al. (1983) reported that a late spring burn reduced or eliminated flowering of the early-blooming species, while flowering in most mid- or late-summer species was unchanged from the control. Leoschke (1986) found that spring burning significantly decreased the percentage of individuals flowering in shooting star. Henderson (1992a) showed a significant negative relationship between the survival of pasque flower buds and the timing of the burn relative to number of days before or after blooming. Plants burned about two weeks prior to blooming had flower bud survival rates of 50 to 75%, while unburned controls had survival rates of 95 to 100%. Hartnett (1991) reported that sexual reproductive effort in western coneflower was significantly lower in prairie burned in the spring than in prairie unburned for four or more years.

Another potentially negative consequence of the burn (whether it occurs early or late in the spring probably does not matter) is the increase in herbivory. The herbivores, most likely rabbits, clearly showed some preferences for plants on the spring burn plots compared to the control plots. It is not specifically known what may have attracted them to the burned plants. Perhaps the regrowth of these plants had higher succulence and palatability compared to un-

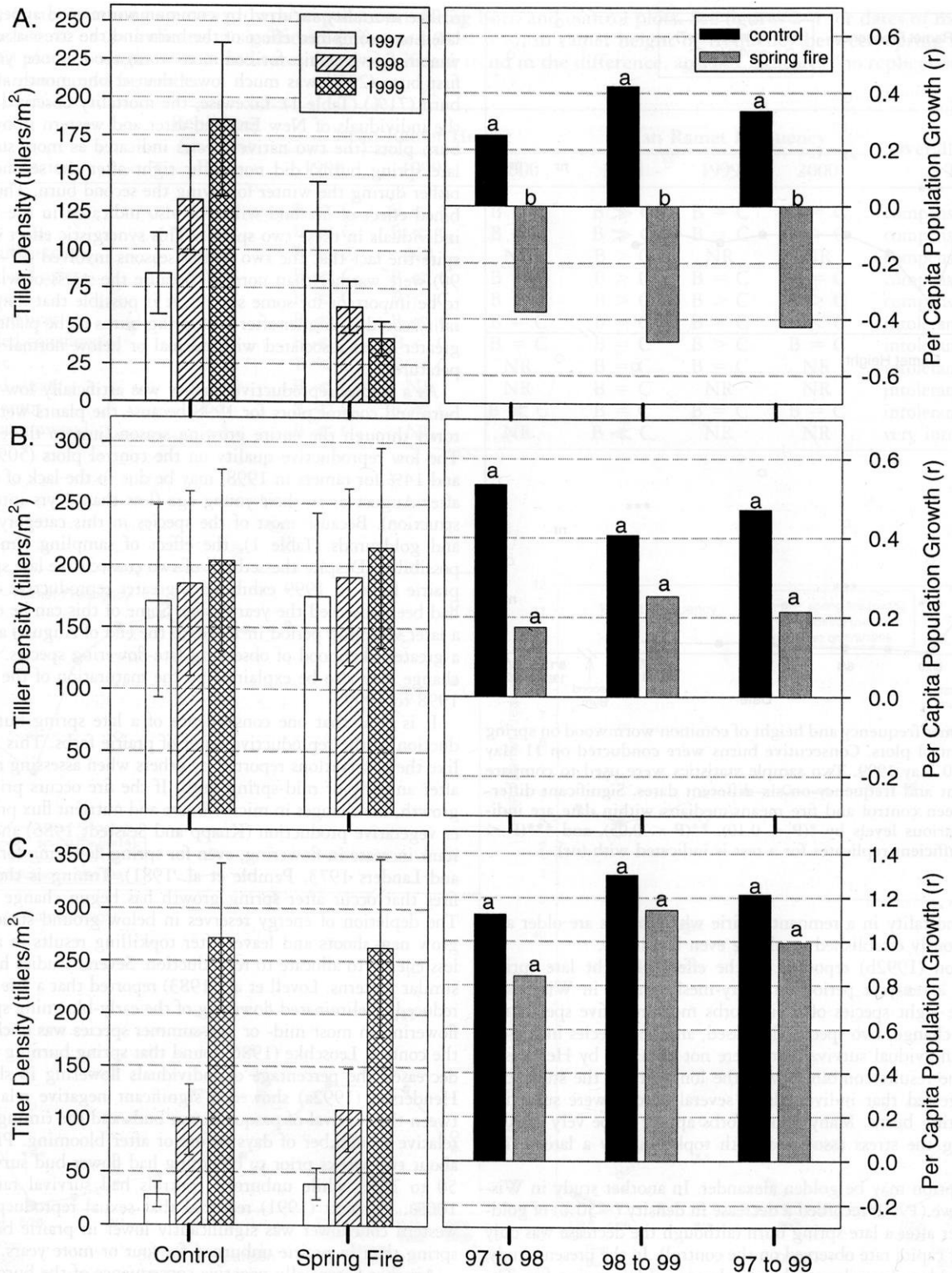


Fig. 5. Mean tiller density in control and spring burn plots in 1997–1999 and per capita growth rates in control and spring burn plots for pairwise comparisons between years for (a) smooth brome, (b) tall fescue, and (c) Kentucky bluegrass. Standard error bars are given for mean tiller density. Significant differences in per capita growth of tillers within a single pairwise comparison are indicated with different letters.

burned plants, or perhaps greater visibility and access (no litter) was a factor. For those species that incurred higher herbivory (e.g., often due to spring fire), there is evidence that the herbivory contributed to lower reproductive quality. In 1999, 12 species exhibited herbivory in at least one of either the burn or control groups, and in 10 of these species, the group with the higher percentage incidence of ramet herbivory also exhibited a lower percentage of ramets in flower. (Pearson correlation between the difference in herbivory [burn - control] and the difference in flowering [burn - control] was -0.61 , $P = 0.035$). The herbivory typically observed resulted in stems cut off at a height of 10 to 20 cm, and these ramets typically did not produce flowers. Spring fires, therefore, may lower reproduction directly by reducing energy allocation to reproductive tissues and indirectly by attracting herbivores to the plants.

A similar herbivory pattern was observed by Henderson (1992a). The potential for herbivory on pasque flower buds was much greater on plants in spring burn plots than on control plots. However, Henderson also observed that plants on spring burn plots were less likely to be eaten by voles than plants on control plots. The removal of litter, important habitat for the voles, directed vole activity away from the burned plants.

There was consistent evidence that ramet height is reduced after a late spring burn. However, some species (Table 5) exhibited a compensatory response by increasing the number of ramets. It is possible that by the end of the growing season this compensatory response might eliminate any differences in the total vigor (i.e., total height of all ramets) between burned and unburned plants. This was true, for example, with ox-eye (Fig. 3). Total plant vigor on 23 July 1998 was not significantly different between the spring fire and control plots (t -test, $P = 0.45$).

Other species did not exhibit a compensatory growth response. Late spring fire had a more negative effect on them because ramet height was decreased, but there was no evidence of increased ramet frequency. For these species (Table 5, intolerant), total plant vigor (biomass) was certainly reduced by the burn. One species, common wormwood, exemplified the highest possible level of stress and loss of vigor due to the late spring fire in that both ramet height and frequency were significantly decreased. This response (Table 5, very intolerant) was presumably a major contributing factor to the significantly high mortality incurred by common wormwood by the end of the study. All seven plants of common wormwood on the burn plots had died after two years, while all five plants on the control plots were still alive (Yates $\chi^2 = 4.8$, $P < 0.05$).

The decreases in ramet height and total plant vigor observed in the intolerant species due to the stress of the late spring burn corroborated the reduction in reproductive quality. Loss of vigor in aboveground organs may be due in part to allocation of energy to rebuild underground storage tissues utilized for regrowth of aboveground tissue after the fire. Since plant survival was very high, changes in prairie species composition are expected to be minimal. However, lower vigor and decreased sexual reproduction are effects of a late spring burn that might have important consequences on prairie community composition over the long term. Lower vigor of aboveground organs could make individual plants less competitive with species that begin growth later in the spring and therefore are less stressed by an early May burn (e.g., warm-season grasses). Although seed production among the perennial prairie plants is not an essential mechanism for species maintenance in the short term, those species with relatively greater seed production should have better opportunities for species maintenance on a site over the long term. Long-term studies of annual spring burns, like Henderson (1992b) and Gibson and Hulbert (1987), provide evidence that the abundance of some forb species is reduced by repeated spring burns. Henderson (1992b) reported significant decreases in prairie violet and

flowering spurge after eight spring burns. Gibson and Hulbert (1987) observed significant decreases in spring forbs such as wild pansy and biscuit root after more than ten years of annual spring burns.

The value of the late spring burn can be seen in the effect on smooth brome. Enormous decreases in smooth brome, especially relative to the increases occurring on the control plots, were observed ($P < 0.001$). By the end of the study, tiller density on the control plots was $4\frac{1}{2}$ times higher than on the spring burn plots. Unfortunately, the same pattern did not occur with either Kentucky bluegrass or tall fescue, although per capita growth rates tended to be lower on the spring burn plots compared to control plots for these species. Nevertheless, the value in the control of smooth brome provided by the late spring fire, when coupled with the high survivorship of prairie forbs, provides a good argument for the claim that the benefits of late spring fires are well worth the reduced growth and flowering that will likely result among the prairie forbs.

The high mortality of common wormwood and the decrease in smooth brome density is encouraging in that it demonstrates that late spring burns can effectively help control non-native species. The difference in the tolerance of late spring fire by a non-native and native species is an important result. It lends support to the proposal that prairie managers should use fire more aggressively when combating non-native species. Prairie species evolved in a fire environment. Managers should use that fact to design prescribed burns that will maximize the role of natural selection and its potential to differentiate between prairie and non-prairie species. By using strategies (e.g., late spring fire during droughts) that impose the harsh prairie environment on non-native species, managers will increase their success in removing them from prairie communities.

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APPENDIX 1. Cross reference of common and scientific names for forb species included in this study or mentioned in the text.

Common Name	Scientific Name (Eilers and Roosa 1994)
azure aster	<i>Aster azureus</i>
biscuit root	<i>Lomatium foeniculaceum</i>
black-eyed susan	<i>Rudbeckia hirta</i>
Canada goldenrod	<i>Solidago canadensis</i>
Canada milkvetch	<i>Astragalus canadensis</i>
common wormwood	<i>Artemisia absinthium</i>
flowering spurge	<i>Euphorbia corollata</i>
frost aster	<i>Aster pilosus</i>
giant goldenrod	<i>Solidago gigantea</i>
golden alexander	<i>Zizia aurea</i>
grey headed coneflower	<i>Ratibida pinnata</i>
Kentucky bluegrass	<i>Poa pratensis</i>
New England aster	<i>Aster novae-angliae</i>
ox-eye	<i>Heliopsis helianthoides</i>
pasque flower	<i>Pulsatilla patens</i>
prairie fleabane	<i>Erigeron strigosus</i>
prairie violet	<i>Viola pedatifida</i>
purple prairie clover	<i>Dalea purpurea</i>
reed canary grass	<i>Phalaris arundinacea</i>
rigid goldenrod	<i>Solidago rigida</i>
rosin weed	<i>Silphium integrifolium</i>
round headed bush clover	<i>Lespedeza capitata</i>
shooting star	<i>Dodecatheon meadia</i>
smooth aster	<i>Aster laevis</i>
smooth brome	<i>Bromus inermis</i>
sweet coneflower	<i>Rudbeckia subtomentosa</i>
tall fescue	<i>Festuca arundinacea</i>
thimble weed	<i>Anemone virginiana</i>
western coneflower	<i>Ratibida columnifera</i>
wester ironweed	<i>Vernonia fasciculata</i>
wild bergamot	<i>Monarda fistulosa</i>
wild pansy	<i>Viola rafinesquii</i>

Fire and Mowing as Management Tools for Conserving a Threatened Perennial and Its Habitat in the Willamette Valley, Oregon

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Sidalcea nelsoniana is a perennial herb native to wetland prairies of the Willamette Valley, Oregon that is listed as threatened under the federal Endangered Species Act and by the State of Oregon. Because of extreme habitat loss and encroachment by woody species and weedy pest plants in remaining wetland prairies, conservation of *S. nelsoniana* will likely require active management of the habitat. This study tests specific hypotheses about the response of *S. nelsoniana* to fire and mowing. During the summer of 1998, aspects of *S. nelsoniana* growth and flowering intensity were measured within 112 permanent quadrats in an established population at W. L. Finley National Wildlife Refuge near Corvallis, Oregon. Elevation, litter depth and cover of woody and other herbaceous species were also measured within each quadrat. The study site was divided into 15 treatment areas, with five replicates of each of the three treatments: burning, mowing and no manipulation. Treatments were applied during the fall of 1998, and the same measurements of *S. nelsoniana* and the surrounding vegetation were recorded in 1999. Re-emergence, growth and flowering intensity of *S. nelsoniana* did not differ significantly among treatments during the first year after manipulations. However, burning and mowing significantly reduced canopy cover and increased herbaceous cover. Because perennials often respond slowly to changes in habitat, treatment effects may be more evident in future years, and long-term monitoring is crucial.

INDEX DESCRIPTORS: *Sidalcea nelsoniana*, fire, mowing, rare plants, habitat restoration, habitat management.

The preservation of pristine areas is of obvious importance for the conservation of rare species. Although many "natural" areas are protected and maintained as preserves by federal, state, or non-profit agencies, these areas are still vulnerable to invasion by non-native pest species. In addition, changes in land use, such as fire suppression, can lead to changes in the structure of plant communities. The prairies of the Willamette Valley, Oregon are prime examples of how changing land use can threaten a habitat and the rare species specific to that habitat.

According to land survey records from around the time of Euro-American settlement, much of the mid-Willamette valley was grassland vegetation, both in the form of low, wetland prairie and upland prairie (Habeck 1961, Johannessen et al. 1971). It is believed that these open areas were maintained for thousands of years by periodic fires carried out by the Kalapuya Indians. As the area was settled, these regular fires ceased (Johannessen et al. 1971), and much of the land was plowed and drained for agriculture. As a result, only a small fraction (<1%) of original Willamette Valley wetland and upland prairie remains.

The existing remnants of open prairie in the Willamette Valley are often threatened by the invasion of woody species or encroachment by non-native herbaceous pest plants. It is in these areas that active habitat management is required to maintain suitable habitat for the survival of native prairie plant populations, including rare species. Previous studies have shown that habitat management, such as burning and/or mowing during the fall, can reduce the cover of woody species and promote native species by restoring an ecological process that has been removed (Clark and Wilson 1996, Wilson and Clark 1997).

The use of habitat management as a tool for the conservation of

rare species requires not only a knowledge of how the treatment will affect the species of concern, but also how the treatment will impact the community as a whole (Lovett Doust and Lovett Doust 1995). *Sidalcea nelsoniana* Piper (Malvaceae, Nelson's checkermallow) is a perennial herb native to wetland prairies of the Willamette Valley and some adjacent areas of the Oregon Coast Range and Cowlitz County, Washington. As of 1998, the distribution of *S. nelsoniana* was limited to only 64 sites, nearly half of which contained fewer than 100 individuals (U.S. Fish and Wildlife Service 1998). Because of this limited distribution and threats to its habitat, *S. nelsoniana* is listed as threatened with extinction under the federal Endangered Species Act and by the State of Oregon (U.S. Fish and Wildlife Service 1993, State of Oregon 1995).

The Endangered Species Act calls for the protection and recovery of population viability of listed species. Habitat restoration plays a key role in this task (Falk 1990, Soulé 1991, Wilson et al. 1992, Sinclair et al. 1995). Like much of the remaining prairie habitat in the Willamette Valley, the habitats of *S. nelsoniana* are changing because of the invasion and growth of woody plants or herbaceous pest plants like *Phalaris arundinacea* L. (reed canarygrass). Effective management will probably require active manipulation of *S. nelsoniana* habitat. Unfortunately, the effects of habitat manipulations on *S. nelsoniana* are untested, and little conclusive information is available about the habitat requirements of this species. In particular, it is unclear how well *S. nelsoniana* adults and seedlings can tolerate shade and other competitive pressures (U.S. Fish and Wildlife Service 1993, Glad et al. 1994).

This study evaluated the effectiveness of potential restoration techniques for *S. nelsoniana* habitat. Specifically, we investigated the effects of prescribed burning and mowing on *S. nelsoniana* and its habitat. Our analysis and interpretation of results considered both immediate effects on the *S. nelsoniana* population (re-emergence and

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growth of above-ground vegetation) and future population trends (flowering intensity, seed production, and levels of seed predation by a native weevil, *Macrobaptus sidalceae* Sleeper).

In addition, because burning and mowing may affect *S. nelsoniana* directly or indirectly through concurrent changes in the surrounding vegetation, we quantified the neighboring vegetation along with aspects of *S. nelsoniana* vigor. This allowed us to test for effects of the manipulations and to investigate the mechanisms causing these results. Ultimately, this research approach should provide information for this study site and suggest more general recommendations for *S. nelsoniana* management.

METHODS

Study Species

Sidalcea nelsoniana is a gynodioecious species that can propagate from either rhizomes or seeds. Reproductive individuals have 30 to 100 cm tall flowering stalks terminating in spikelike inflorescences of pinkish-lavender to pinkish-purple flowers (U.S. Fish and Wildlife Service 1993). Peak flowering occurs mid-June through mid-July in the Willamette Valley. The fruits are several-seeded schizocarps and mature in late July and early August. *S. nelsoniana* is most often found in wetland prairies, ash swales, streamsides, and roadside ditches.

Study Site

One of the largest populations of *S. nelsoniana* is found at William L. Finley National Wildlife Refuge (NWR), 16 km south of Corvallis in the Willamette Valley, Oregon, USA. Invasion and growth of woody plants or herbaceous pest plants like *P. arundinacea* are likely causes for some apparently precipitous declines in *S. nelsoniana* numbers at Finley NWR (Maura Naughton, pers. comm.). The study population of *Sidalcea nelsoniana* is located within the refuge in a riparian hedgerow between two agricultural fields planted with perennial rye grass. The hedgerow runs east-west and is approximately 750 m long by 50 m wide. The elevation difference between the highest and lowest measurement quadrats is approximately 7.1 m. The east end of the site floods to approximately 20 cm above the soil surface from November through April, while the west end of the site remains unflooded throughout the year (Bartels 2000).

The dominant vegetation of this site includes *Festuca arundinacea* Schreb. (tall fescue), *Vicia* spp., *Rubus discolor* Weihi & Nees (Himalayan blackberry), and *Rubus macrophyllus* Weihi & Nees (large leaved blackberry) at the driest end, with *P. arundinacea*, *Phalaris aquatica* L. (Harding grass) and *Carex* spp. dominating in the wettest portion of the site. *Fraxinus latifolia* Benth. (Oregon ash) is found throughout (nomenclature follows Hitchcock and Cronquist 1973). *Sidalcea nelsoniana* individuals are scattered throughout the length of the site, sometimes growing under full sun and sometimes under heavy shade. The soil at the site is Waldo silty clay loam, while soils in the surrounding agricultural fields are classified as Coburg silty clay loam and Amity silt loam (Soil Conservation Service 1975).

The region experiences a modified maritime climate with cool, wet winters and warm, dry summers. Average annual precipitation as recorded in Corvallis is 108.5 cm, with 93.0 cm occurring October through April. Average minimum and maximum temperatures are 0.6°C and 7.5°C in January and 10.6°C and 26.8°C in July (Oregon Climate Service 1990).

Experimental Design

Because of the spatial heterogeneity of the site and logistical constraints in applying treatments, typical experimental designs were impractical. Rather, the study was designed to investigate the vigor

Table 1. Stratification scheme based on pre-manipulation conditions for application of experimental manipulations. Approximately 10 quadrats centered on *Sidalcea nelsoniana* plants were placed in each of the 12 combinations.

	Extensively Flooded	Not Extensively Flooded
Woody plants dense	Burned Mowed Control	Burned Mowed Control
Woody plants not dense	Burned Mowed Control	Burned Mowed Control

of *S. nelsoniana* under both experimentally manipulated conditions (prescribed burning and mowing) and a range of pre-existing conditions of woody plant cover and hydrology using General Linear Modeling (McNeil et al. 1996) as the tool for statistical analysis.

During the spring of 1998, the site was surveyed and *S. nelsoniana* individuals were marked and categorized into strata according to pre-manipulation density of woody plant cover and general hydrologic conditions (Table 1). Flooding and woody plant cover were described categorically only for the purposes of stratifying the manipulations. Analysis of the effects of these variables on *S. nelsoniana* used actual measurements of flooding and woody plant cover. A total of 347 *S. nelsoniana* plants were marked throughout the site. Of these, 25 were vegetative and 322 were reproductive, as indicated by the presence of flowering stalks. Only reproductive individuals were included in the study.

Of the reproductive individuals, 30 plants were randomly selected (using a random number generator) from each of the pre-manipulation strata for a total of 120 plants. A 0.5-m² quadrat was centered on each selected individual. These plant-centered quadrats were the observational units in the study. Due to practical difficulties with quadrat-sized burns, the site was divided into fifteen treatment areas that encompassed varying numbers of quadrats. Treatments were randomly assigned to each area with slight adjustment to balance the number of quadrats in each of the 12 treatment-by-condition strata (Table 1).

Because of the extent of the site, three "pseudoblocks" were assigned along the length of the site. The boundaries were assigned where there was a gap of at least 20 m between the two closest *S. nelsoniana* plots and so that each pseudoblock included at least one replicate of each of the three treatments.

Vegetation Measurements

Pre-manipulation conditions were recorded within each quadrat between 26 June 1998 and 7 July 1998. The same characteristics were measured for post-manipulation conditions between 5 July 1999 and 12 July 1999. Measurements of *S. nelsoniana* included size (as cover), number of flowering stalks, number of inflorescences by type (pistillate or perfect) and height of the tallest flowering stalk. Measurements of the surrounding vegetation included litter depth, woody canopy cover (above 1.5 m) and cover by two species groups (herbaceous and woody less than 1.5 m in height) within two vertical strata (above and below *S. nelsoniana* mid-height [40 cm]). Woody canopy cover was estimated from the north side of the quadrat using a spherical densiometer held approximately 1.5 m above the ground so that measurements emphasized canopy cover from the south. Cover of *S. nelsoniana* and surrounding herbaceous and woody vegetation

was estimated by consensus of two investigators using calibration templates.

Seed Production Measurements

Seed production and levels of weevil damage were measured during early August in 1998 and 1999. For each quadrat, two infructescences were randomly selected and the number of fruits per infructescence was recorded. One randomly selected fruit from each quadrat was examined under a dissecting microscope to determine the number of filled, undeveloped, and weevil damaged seeds using the criteria established by Gisler and Meinke (1997).

Hydrologic Measurements

Because the hydrologic impact on wetland plants is largely determined by the timing and duration of flooding, hydrologic impacts on *S. nelsoniana* were characterized through the use of elevation surveys and site observations throughout the fall, winter and spring as described in Bartels (2000). Elevation is often correlated with soil moisture (Nelson and Anderson 1983) and was used to quantify the relative hydrologic impact on each *S. nelsoniana* measurement plot.

Manipulations

Prescribed burning and mowing manipulations were conducted 10–11 September 1998 by U. S. Fish and Wildlife Service personnel. Treatment areas ranged between 10 and 30 m in width by 25 to 50 m in length, with a buffer of at least 1 m between the treatment edge and the nearest measurement quadrat. For adequate replication, there were five areas of each manipulation and five unmanipulated areas that served as controls.

Convection burns were ignited at the southwest corner of each burn treatment area. Flames burned for 5 to 20 minutes after ignition, with average flame heights between 0.5 and 2 m. In areas with thick vegetation, flames often shot into the ash canopy. In similar prairies, experimental-scale fires have been shown to closely approximate the behavior of large-scale fires (Maret 1996).

Within each mowing treatment area, herbaceous vegetation and shrubs were mowed with a 4.5 m-wide tractor mower to approximately 15 cm above the soil surface. Large trees were cut with a chain saw and all woody brush was removed from the site.

Statistical Analysis

The effects of manipulations on *S. nelsoniana* were analyzed by comparing the explanatory power of a series of statistical models as outlined by McNeil et al. (1996). The analysis followed a mixed design of planned manipulations, unplanned pre-manipulation conditions, and conditions modified by manipulations. Response variables were measurements of *S. nelsoniana* vigor including re-emergence, growth (cover), flowering intensity (number and height of flowering stalks and total number of inflorescences), and weevil damage. Values for cover, number of flowering stalks and number of inflorescences were square root transformed prior to analysis to meet the assumptions of the statistical models. Seed production was not evaluated statistically because of low seed production in 1999. Explanatory variables included categorical variables for treatment, pseudoblock and flowering type, and quantitative variables of elevation and the 1998 measurements of canopy cover, woody and herbaceous cover in two vertical strata, and litter depth. All quantitative explanatory variables except low herbaceous cover and litter depth were rank transformed prior to analysis. The pre-manipulation value of *S. nelsoniana* vigor served as a covariate in the analyses. The individual models used are described in detail below.

Of the 120 plots originally measured in 1998, seven could not be

relocated in 1999. Additionally, one plot was missed when manipulations were applied and was therefore excluded from the analyses. The complete data set used in the analyses consisted of 112 measurement plots.

The first step in evaluating the hypotheses was to determine whether the treatments had an effect on *S. nelsoniana* vigor (growth, flowering intensity, and weevil damage) after accounting for differences in the pre-existing conditions of shading, crowding, and hydrology (as measured by elevation). Each aspect of *S. nelsoniana* vigor was used as the response variable in a series of models designed to test whether the treatments explained a significant amount of the variation in that variable. The full model, consisting of each explanatory variable and the covariates (Table 2) as well as all possible pairwise interactions among the variables, was compared to a restricted model, from which all terms involving treatment were dropped, using a generalized F-test (McNeil et al. 1996). This analysis approach tests for both direct treatment effects and indirect effects of the treatment through interactions with the environment. The mechanisms were explored by evaluating the outcome of the tests for treatment effects on the surrounding vegetation.

ANOVAs were used to test for treatment effects on litter depth, canopy cover, and woody and herbaceous cover both above and below *S. nelsoniana* mid-height. The response variable was the change in cover from 1998 to 1999 with treatment, pseudoblock, and the treatment by pseudoblock interaction as the explanatory variables. The F-ratio was calculated by comparing the treatment mean square to the mean square of the interaction with pseudoblock (Underwood 1997, Newman et al. 1997). Least square means were then compared using Tukey's test (Day and Quinn 1989).

RESULTS AND DISCUSSION

Pre-manipulation Vegetation Characteristics

Although quadrats were centered on *S. nelsoniana* plants, pre-manipulation cover of *S. nelsoniana* (July 1998) within each quadrat averaged only 8.6% (Table 3). Thus, this rare plant, even in this relatively large population, was not a dominant in the vegetation.

The number of pistillate inflorescences outnumbered the number of perfect inflorescences by 3.5 to 1. Pistillate to perfect flower ratios in other Willamette Valley *S. nelsoniana* populations ranged between 0.2:1 and 5.0:1 (Steve Gisler, pers. comm.). Pollen availability could limit seed production in populations with high ratios of pistillate to perfect flowering types.

In 1998, 11% of all carpels collected contained filled seeds, while 39% contained unfilled seeds and 51% were completely or partially destroyed by weevils. These rates are similar to the weevil infestation rates found by Gisler and Meinke (1997) across 15 *S. nelsoniana* populations.

Herbaceous cover below *S. nelsoniana* mid-height (40 cm) was often dense and averaged 45.6%. As would be expected, herbaceous cover above *S. nelsoniana* mid-height was less dense, averaging 15.3%. Woody cover below *S. nelsoniana* mid-height was relatively sparse, averaging 3.2%. Above *S. nelsoniana* mid-height (and below 1.5 m), woody cover averaged 8.7%. Average canopy cover was 23.3%, and litter depth averaged 5.4 cm (Table 3).

Post-manipulation Vegetation Characteristics

One year after manipulations (1999), the average cover of *S. nelsoniana* across all quadrats remained at 8.6% (Table 3). Average cover of *S. nelsoniana* by treatment area (not adjusted for pre-manipulation condition) was 6.9% in burned areas, 9.4% in mowed areas and 9.6% in unmanipulated controls (Table 3). These averages represented an increase of less than 1% over the 1998 measurements in

Table 2. Variables (and transformations) used in the general linear models testing for treatment effects on *Sidalcea nelsoniana* growth and flowering intensity. All measurements were within *S. nelsoniana*-centered quadrats.

Response variables. <i>Sidalcea nelsoniana</i> vigor after manipulation.
Vegetative cover (square root)
Number of flowering stalks (square root)
Number of inflorescences (square root)
Height of flowering stalks
Seed production ^a
Weevil damage ^b
Explanatory variables and covariates
Treatment (burning, mowing, or unmanipulated control)
Pseudoblock (1, 2, or 3 based on location along the site)
Relative elevation (rank)
Cover of herbaceous plants (<40 cm stratum) before manipulation
Cover of herbaceous plants (>40 cm stratum) before manipulation (rank)
Cover of woody plants (<40 cm stratum) before manipulation (rank)
Cover of woody plants (40–150 cm stratum) before manipulation (rank)
Woody canopy cover (>150 cm) before manipulation (rank)
Litter depth before manipulation
Associated measure of <i>S. nelsoniana</i> before manipulation
Flower type (pistillate or perfect)

^aSeed production was not tested due to extremely low seed production in 1999

^bTreatment and flower type were the only explanatory variables included in this analysis

the mowed and unmanipulated areas and a decrease of less than 1% in the burned areas. Therefore, they are unlikely to be biologically significant.

The number of flowering stalks averaged 5.1 per quadrat in 1999 (Table 3), and the unadjusted average was also similar among treatments and years (Table 3). The number of inflorescences and the height of the flowering stalks generally decreased from 1998 to 1999 overall and across all treatments (Table 3). The flowering type ratio was even more skewed toward pistillate plants in 1999 (5.7:1) and was higher than ratios observed in other Willamette Valley populations (Steve Gisler, pers. comm.).

S. nelsoniana fruits produced an average of seven carpels each in 1999, just as in 1998. Seeds were unavailable from 20% of the measurement plots because they had either already dispersed or because the plant did not produce fruits. Of those that produced fruits in 1999, less than 1% of the carpels collected contained filled seeds, and 74% had been damaged by weevils. The remaining 25% contained undeveloped or unfilled seeds. Other *S. nelsoniana* populations also experienced higher than average rates of weevil damage in 1999 (Steve Gisler, pers. comm.).

Herbaceous cover both below and above *S. nelsoniana* mid-height was more dense in 1999, especially in the burned and mowed areas (Table 3). Woody cover below *S. nelsoniana* mid-height increased in 1999 in all treatment areas, but this increase was greatest in control plots (Table 3). Woody cover between 40 and 150 cm and canopy cover increased between 1998 and 1999 in unmanipulated areas but decreased sharply in burned and mowed areas (Table 3).

Hypothesis Tests: Treatment Effects on *Sidalcea nelsoniana*

Re-emergence of above-ground vegetation. Re-emergence of marked plants was high across all treatments. Above-ground vegetation was present in 108 out of 112 marked individuals one year after manipulations. Re-emergence was similar among the treatments: 97.3% in burned areas (36/37), 97.1% in mowed areas (34/35) and 95.0% in controls (38/40). These results support the null hypotheses that neither fire nor mowing have a direct effect on the re-emergence of *S. nelsoniana* above-ground vegetation.

Growth and flowering intensity. Treatment did not explain a significant amount of the variation in *S. nelsoniana* cover ($F_{24,22} = 1.55$, $P = 0.15$), number of flowering stalks ($F_{24,22} = 0.71$, $P = 0.79$), flowering stalk height ($F_{24,22} = 0.97$, $P = 0.53$), or number of inflorescences ($F_{24,22} = 0.64$, $P = 0.86$) after accounting for the covariates and pre-existing conditions of hydrology and surrounding vegetation. These results support the null hypotheses that neither fire nor mowing has an effect on *S. nelsoniana* growth or flowering intensity during the first year after manipulations.

Seed production. Because of the small number of seeds produced overall (less than 1% of the total carpels collected contained filled seeds), we did not test for treatment differences in seed production. However, the low seed production across all treatments supported the null hypotheses that fire and mowing had no effect on *S. nelsoniana* seed production.

Weevil damage. Statistical analyses of weevil damage were done using only those 90 individuals for which fruits were available. The percentage of carpels damaged by weevils did not differ significantly among treatments after adjusting for the flower type of the individual ($F = 0.35$ for treatment, $P = 0.70$). This supported the null hypotheses that neither fire nor mowing had a direct effect on weevil damage in *S. nelsoniana*.

Treatment Effects on the Surrounding Vegetation

Woody cover. Treatments had significant effects on canopy cover one year after application ($F_{2,4} = 28.5$, $P < 0.01$, Fig. 1a). Canopy cover increased slightly in the unmanipulated areas from 1998 to 1999 but decreased significantly in both the burned and especially the mowed areas (Fig. 1a). The more pronounced decrease in the mowed areas was not surprising because trees were actually removed from the mowed areas and would be unlikely to sprout to canopy height in just one season. Trees in the burned areas were not removed and could leaf out again where the fire was not intense enough to kill the entire tree.

Although both the raw and square-root adjusted means showed a decrease in woody cover between 40 and 150 cm in the burned and mowed areas and an increase in the controls (Table 3, Fig. 1a), the

Table 3. Raw means (and standard errors) of *Sidalcea nelsoniana* (a) and surrounding vegetation (b) measurements before (1998) and after (1999) burning and mowing manipulations were applied. n = number of plots in each treatment.

a)	Overall (n = 112)		Burn (n = 37)		Control (n = 40)		Mow (n = 35)	
	1998	1999	1998	1999	1998	1999	1998	1999
Cover (%)	8.6 (0.5)	8.6 (0.6)	7.3 (0.7)	6.9 (0.8)	9.3 (0.8)	9.6 (1.1)	9.2 (0.9)	9.4 (1.2)
Flowering stalks (#)	5.7 (0.5)	5.1 (0.5)	5.2 (0.7)	4.2 (0.5)	5.1 (0.6)	5.4 (0.9)	6.9 (1.1)	5.7 (0.8)
Inflorescences (#)	27.3 (2.5)	15.2 (1.8)	24.8 (4.5)	14.1 (2.5)	28.3 (4.2)	14.5 (3.0)	31.2 (5.0)	17.7 (3.6)
Flower stalk ht. (cm)	114.7 (2.3)	78.6 (3.4)	112.4 (3.6)	80.5 (5.8)	116.5 (3.5)	80.2 (5.6)	115.0 (4.8)	74.9 (6.3)

b)	Overall (n = 112)		Burn (n = 37)		Control (n = 40)		Mow (n = 35)	
	1998	1999	1998	1999	1998	1999	1998	1999
Herbaceous cover (%):								
Below 40 cm	45.6 (2.3)	69.0 (1.8)	42.7 (3.8)	75.4 (2.7)	44.7 (3.5)	58.7 (3.4)	49.7 (4.6)	74.1 (2.5)
Above 40 cm	15.3 (1.0)	43.4 (2.5)	15.4 (1.8)	53.7 (4.2)	13.0 (1.3)	28.8 (3.8)	17.7 (1.9)	49.3 (3.9)
Woody cover (cm):								
Below 40 cm	3.2 (0.5)	5.5 (0.9)	3.6 (0.8)	5.1 (1.2)	4.3 (1.0)	8.4 (1.8)	1.6 (0.6)	2.6 (1.0)
40–150 cm	8.7 (1.4)	8.6 (1.6)	12.0 (2.9)	6.3 (1.6)	9.7 (2.7)	15.9 (3.8)	3.9 (1.1)	2.8 (1.1)
Canopy	23.3 (2.7)	14.5 (2.3)	23.2 (4.7)	7.3 (1.7)	23.3 (4.4)	32.7 (5.0)	23.3 (5.2)	1.3 (0.7)
Avg. litter depth (cm):	5.4 (0.3)	6.0 (0.3)	4.9 (0.4)	5.5 (0.6)	5.9 (0.4)	5.2 (0.3)	5.3 (0.5)	7.5 (0.6)

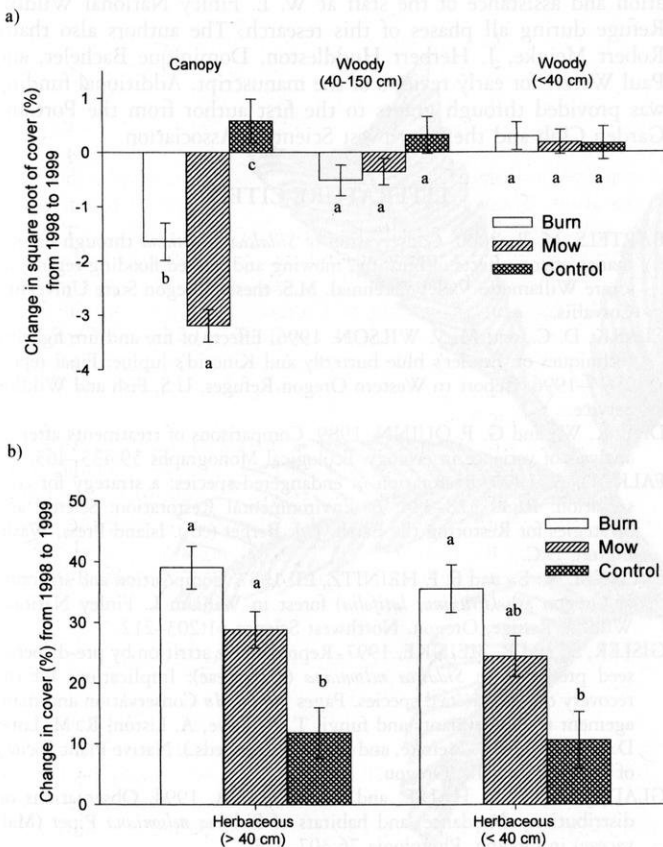


Fig. 1. Least square means and standard errors for change in canopy cover and woody cover above and below *S. nelsoniana* mid-height (a) and change in herbaceous cover above and below *S. nelsoniana* mid-height (b) from 1998 to 1999 by treatment. Values are the square root of the 1999 cover measurement subtracted from the square root of the 1998 cover measurement. Treatments that share the same letter are not statistically different from one another (Tukey's HSD, P = 0.05).

treatment effect was not statistically significant ($F_{2,4} = 2.0$, $P = 0.26$, Fig. 1a). The species in this category were primarily shrubs such as rose and blackberry, which often resprout after manipulations (Wilson and Clark 1997). In addition, many of the ash trees that were cut in the mowed treatments resprouted to approximately 1 m, adding cover to this intermediate height category. If repeated applications of the treatments diminished resprouting, differences in woody shrub cover would likely be more pronounced.

Woody cover below 40 cm increased slightly in all areas and was not significantly affected by the manipulations ($F_{2,4} = 0.1$, $P = 0.94$, Fig. 1a). Once again, repeated applications of the treatments may eventually kill the woody vegetation and reduce the cover in this category.

Herbaceous cover. Herbaceous cover above 40 cm was significantly affected by the treatments ($F_{2,4} = 12.5$, $P = 0.02$). While herbaceous cover increased in all areas from 1998 to 1999, the increase was greater in burned and mowed plots than in unmanipulated controls (Fig. 1b). The more frequent occurrence of *Vicia* spp. as the dominant vegetation in the plots during 1999 likely accounted for much of this increase (dominant in 56% of plots in 1999 compared to only 4% in 1998, Bartels 2000).

The increase in herbaceous cover below 40 cm in 1999 was also affected by the treatments ($F_{2,4} = 8.4$, $P = 0.04$). The burned treatment was significantly greater than the control while the mow treatment was intermediate to the burn and control treatments (Fig. 1b).

Litter depth. Treatment had no significant effect on average litter depth ($F_{2,4} = 1.0$, $P = 0.45$ for treatment). Although there was a significant interaction between treatment and pseudoblock ($F_{4,103} = 2.6$, $P = 0.04$), graphical inspection of this interaction showed no clear trend of treatment effect on litter depth.

Mechanisms

Although burning and mowing did not significantly affect *S. nelsoniana* vigor during the first year after manipulations, both fire and mowing did alter the surrounding vegetation. However, the specific changes that occurred in this first year after treatments may have acted in opposing directions to result in no net change in *S. nelsoniana* growth and flowering intensity.

As in other studies (e.g. Clark and Wilson 1996), both fire and mowing were effective at reducing woody cover as compared to controls. Because *S. nelsoniana* plants are often found growing in full sun, it seems unlikely that a reduction in woody cover would be harmful to *S. nelsoniana* vigor. Therefore, this reduction in shading should either promote or have no effect on *S. nelsoniana* growth and reproduction.

The large increase in herbaceous cover in burned and mowed plots compared to controls in the first year after treatments is less well documented (but see Kost and De Steven 2000). Because herbaceous cover also increased in the controls, some of the increase was likely due to year to year variation in climate (such as the unusually wet winter and spring in 1999). However, herbaceous cover increased significantly more in the treated areas. Thus, the herbaceous vegetation may have been stimulated by the increased light in burned and mowed areas. It is also possible that the additional increase was a response to nutrient mineralization caused by the burning and mowing treatments. If nutrients were mineralized by the treatments, *S. nelsoniana* would be expected to increase as well. However, if the increased nutrients were utilized more efficiently by the surrounding vegetation, competition may have limited *S. nelsoniana* growth and flowering intensity.

Although it is difficult to tell from these data how the surrounding vegetation affects *S. nelsoniana* vigor, many species respond positively to a suppression of the surrounding vegetation (Howe 1999). Therefore, it could be assumed that a decrease in canopy cover or the surrounding vegetation would lead to decreased competition for light and/or nutrients and result in an increase in *S. nelsoniana* growth and/or flowering intensity. Similarly, an increase in the surrounding vegetation could lead to increased competition and decreased *S. nelsoniana* vigor. If only one of these changes had occurred, the results may be easier to interpret. However, in this case, *S. nelsoniana* plants that may have been able to take advantage of an opened canopy might have instead been outcompeted by other herbaceous plants.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

It is not surprising that direct treatment effects were not apparent during the first year after manipulations. Experimental habitat manipulations often do not produce strong patterns until several years after treatment application (Wilson and Clark, in press). The characteristics of the surrounding vegetation in 1998 (before manipulations) explained much of the variation in *S. nelsoniana* vigor in the following year (restricted models had R^2 values from 63.5 to 78.7%, Bartels 2000). This suggests that the characteristics of the surrounding vegetation in 1999, the environment as altered by the manipulations, may be very important in influencing the growth and flowering intensity of *S. nelsoniana* in subsequent years. Because neither burning nor mowing killed *S. nelsoniana* or significantly harmed the growth or reproduction of the species, treatments were reapplied during September 1999 and measurements of *S. nelsoniana* and the surrounding vegetation were recorded again during the summer of 2000.

While the impact of the reduction in woody cover on *S. nelsoniana* vigor is unclear at this point, reduction in woody cover is a key goal in the restoration and management of wetland prairie areas, as few species can survive under thick shrub cover. Furthermore, because shrubs and trees often resprout after burning or mowing, treatments must be repeated regularly for the most efficient control of woody cover (Frenkel and Heinitz 1987, Wilson and Clark 1997).

Additionally, there may be some delay between the mineralization of nutrients caused by fire and/or mowing and the ability of *S. nelsoniana* to take up these resources and utilize them for increased

growth or flowering intensity. The constraints of working with a protected species prevented this study from comparing below ground productivity among the three treatment conditions. Perhaps in this first year after manipulations, the increased resources were primarily stored below ground and did not result in a biologically or statistically meaningful increase in above-ground cover. As woody cover is further reduced by repeated applications of the treatment, conditions may become more favorable for additional above-ground production that would enable *S. nelsoniana* to better compete with the surrounding herbaceous vegetation.

Many mechanisms seemed to influence *S. nelsoniana* vigor in this system. With repeated treatment application, one or more of these processes may emerge as being more important than the others, and the relationship between fire, mowing, and the growth and flowering intensity of mature *S. nelsoniana* individuals may become more clear. Furthermore, additional management efforts may be necessary to control the surrounding herbaceous vegetation and reduce the competitive pressure on *S. nelsoniana*. These results reinforce the importance of careful long term monitoring in any habitat management program.

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Changes in Density and Height of the Shrub *Baccharis halimifolia* Following Burning in Coastal Tallgrass Prairie

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In the absence of fire, coastal tallgrass prairie often becomes increasingly dominated by shrubs, with one of the most prevalent of these being *Baccharis halimifolia* L. (eastern baccharis). In this study, we monitored the response of *B. halimifolia* to burning at the Brazoria National Wildlife Refuge in Texas. The primary objective of this study was to evaluate both the short-term response of *B. halimifolia* to burning and to estimate the rate at which this species recovers its preburn density and shoot height. Plots (10 × 10 m) containing *B. halimifolia* were established in June of 1997 at 11 sites that were slated for prescribed burning. Nine sites were burned in the summer of 1997, and two were burned in the spring of 1998. Shoot density and height were measured before and after burn events. Mean shoot density decreased by 43% immediately after burning and was still 47% below the original density one year after the burn. Mean plant height was initially reduced by 68% compared to the preburn height. One year after burning, height was 43% below preburn levels. Despite the overall reduction in density and height, the recovery of *B. halimifolia* following burning was highly variable among plots. These results suggest that fire can substantially reduce the density of *B. halimifolia*; however, high site-to-site variability indicated that additional factors are important and that further, more refined studies are needed.

INDEX DESCRIPTORS: woody plant, prescribed fire, coastal prairie, succession.

Coastal prairie is a mid- to tallgrass prairie ecosystem that once covered an estimated 3.4 million ha in the U. S. It extends from southcentral Louisiana to south Texas, being bordered on the south by coastal wetlands and on the north by a variety of forest types. It occurs primarily on soils classified as vertisols, mollisols, and alfisols. Vertisols are the most widespread and have characteristic microknolls and microdepressions called gilgai. Prairies located on alfisols often have mima mounds, topographic features that vary from 2–20 m across and up to 1.5 m tall (Cain 1974, Smeins et al. 1991). Prairies on higher elevations (upland prairies) are dominated by *Schizachyrium scoparium* (Michx.) Nash (little bluestem) and *Sorghastrum nutans* (L.) Nash (indiangrass), with *Panicum virgatum* L. (switchgrass) and *Tripsacum dactyloides* L. (eastern gamagrass) becoming dominant in low areas (wet prairie). In areas where prairie and salt marsh intergrade (salty prairie), *Spartina spartinae* (Trin.) Hitchc. (gulf cordgrass) becomes the dominant graminoid. *Andropogon gerardii* Vitman (big bluestem) is present in moist, sandy soils, but it is less common than in more northern tallgrass prairie. *Paspalum plicatulum* Michx. (brownseed paspalum) is an important and conspicuous part of the vegetation of the upper coastal prairie north of the San Antonio River, while *Sporobolus asper* (Michx.) (meadow dropseed) Kunth replaces it in the lower coastal prairie (Smeins et al. 1991). A varied forb component fills out this grass matrix, creating one of North America's most diverse ecosystems. In Louisiana alone, more than 600 species have been collected in prairie remnants, with more than 900 species reported for the entire range of coastal prairie (Allen and Vidrine 1989, Allain and Castille 2001). Primarily due to agriculture and cattle grazing, less than 1% of climax coastal prairie remains intact today. It is considered to be one of the most endangered plant communities in North America (Diamond et al. 1992, Grace et al. 1999).

Several woody species colonize coastal prairie due to disturbance and/or the absence of fire. Of these, the most common is *Baccharis*

halimifolia L. (eastern baccharis), a native, dioecious, perennial shrub that grows to 4 m tall, often forming dense colonies. *B. halimifolia* occurs along the Atlantic and Gulf coasts of North America from Massachusetts to Texas and into Mexico. It is most common on the southeastern Coastal Plain, extending as far inland as Arkansas and the central Piedmont Plateau (Duncan et al. 1957, Duncan and Duncan 1988, Patton and Judd 1988, Krischik and Denno 1990a, b). It occurs in open forests, beaches, wet prairie, swamps, marshes, and, due to a high tolerance of salt spray, along the fringe of brackish marshes (Penfound and Hathaway 1938, Oosting 1954). Site affinities indicate that *B. halimifolia* typically grows in moist soils with a high organic content (Egler 1952, Duncan and Duncan 1988, Barbour and Billings 1988).

A successional species that rapidly invades disturbed grasslands, *B. halimifolia* appears to have become more common over its historic range in response to human influences (Penfound and Hathaway 1938, Allen 1950, Scifres et al. 1993). It has been introduced into Australia and the Mediterranean region of Europe, where it is a major pasture weed (Haseler 1969, Westman et al. 1975). As of 1973, *B. halimifolia* had colonized 81,720 ha in east and southeast Texas (unpubl. records, USDA Soil Conservation Service, Tempel, TX). *B. halimifolia* invades coastal prairie in Louisiana and Texas where it has been shown to reduce herbaceous diversity (Harcombe 1989). While it can be controlled with herbicides and mowing, these practices are expensive and can have unwanted consequences on the plant and animal communities. Mimicking the role of the natural fire regime, prescribed fire is often used to control *B. halimifolia* in coastal prairie. However, observations on its susceptibility to fire vary (Leenhouts and Baker 1982, Grelen 1975, 1983, Miller and Miller 1999). When burned (or clipped), *B. halimifolia* resprouts readily (DeLoach et al. 1986, authors, pers. obs.). However, there is little published research on the effectiveness of prescribed fire in reducing the abundance of *B. halimifolia*.

Table 1. Study sites at the Brazoria NWR and their major characteristics. Boldface sites were burned during experiment and lightface sites were not. Response type indicates the effect of fire on *Baccharis halimifolia* on a scale of responses: exterminated (1), decimated (2), slow rebound (3), rebound (4), weak affect (5), and stimulated (6). Note that this refuge unit was obtained in 1990, at which time all grazing and much of the cultivation ceased.

Site #	Previously Cultivated	Community Type	Management Since 1990	Burn Date	Response Type
2	no	salty prairie	unmanaged	3/98	4
3	no	salty prairie	mowed su 96	96	3
4	no	salty prairie	mowed su 96	96	3
6	no	salty prairie	unmanaged	8/97	3
7	yes	old-field	unmanaged	8/97	3
8	yes	upland prairie	trees herbicided	8/97	3
9	yes	upland prairie	wildfire/mowed 96	96	*
11	no	mima mound	burned 96	96	6
13	no	wet prairie	unmanaged	7/97	2
14	no	upland prairie (mima mound)	burned 95	3/98	4
18	no	upland prairie	burned sp 97	2/97	5
19	yes	old-field	burned 95	8/97	1
20	yes	old-field	mowed 96	96	2
21	yes	old-field	burned sp 97	97	4
22	yes	old-field	unmanaged	7/97	2
23	yes	old-field	unmanaged	7/97	3
24	yes	old-field	burned 96	7/97	4
25	yes	old-field	burned 97	96	4
26	no	salty prairie	unmanaged	8/97	3

* Data discarded due to stem density too great to count

In this study, our objective was to characterize the response of *B. halimifolia* to prescribed fire, both immediately and for a period after being burned. It was not deemed feasible in this study to establish and maintain unburned control plots at each site because of the logistics that would be involved. First, the sites are spread across a largely roadless landscape, and many are only accessible by marsh buggy, making the maintenance of fire breaks by mowing and fire retardant foam (as in King and Grace 2000) difficult. Second, maintenance of fire breaks in this system typically involves repeated disking of the soil, which we considered to be an unacceptable level of impact on what is one of the most extensive remnants of virgin coastal prairie remaining. For these reasons, our approach was to monitor the dynamics and recovery of *B. halimifolia* before and after burning using a repeated-measures protocol. It is recognized that this approach is somewhat limited for addressing hypotheses about the long-term effects of burning, but we feel that it is adequate for documenting abrupt change and recovery following fires.

METHODS

This research was conducted at the Brazoria National Wildlife Refuge (NWR) near Angleton, Texas at approximately 29° N, 95° W. The study was conducted in the northern part of the refuge, which was historically coastal prairie. The sites studied ranged from salty prairie dominated by *Spartina spartinea* (Trin.) Merr. ex A. A. Hitchc. (gulf cordgrass) to upland prairie dominated by *Schizachyrium scoparium* (Michx.) Nash (little bluestem). In June 1997, paired 10 × 10 m plots were established at 26 sites to monitor changes in vegetation resulting from management practices. Pairs of plots were established at each site to evaluate the degree of within-site variability in *B. halimifolia* dynamics. Twenty of the 26 sites contained *B. halimifolia*. Nine of the sites containing *B. halimifolia* were burned in the summer of 1997 shortly after plot establishment, and two more were burned in the spring of 1998. One of these 11 sites was

located on a mima mound. Of the remaining sites, eight had been burned before the study was initiated. Examination of management histories of the sites revealed that of the 11 sites that were burned during the course of our observations, three were salty prairie, two were upland prairie (one on a mima mound), one was wet prairie, and five were oldfields (Table 1).

Shoot density and height of individual plants of *B. halimifolia* were measured in July 1997, October 1997, April 1998, July 1998, and October 1998, although individuals were not tagged. Height was measured to the nearest cm.

Data were analyzed using SAS (SAS Institute 1996). Degree of within-site variability was examined for the pairs of plots at each site. Because paired plots were very similar and subjected to similar growth and burn conditions, within-site variability was not observed to be significant (i.e., subplot behavior was virtually identical), and the data for each set of paired plots were averaged to produce a single value for each site.

The 11 sites burned during the monitoring period were analyzed for mortality and recovery of *B. halimifolia* after being subjected to fire. The change in plant density (DEN), average height (AVGHT), and total height (TOTHT) was compared for time 1 (prefire), time 2 (postfire), and time 3 (final). Repeated measures analysis of variance was used to test for the statistical significance of changes over time in stand density, average plant height, and total height per plot. Using this procedure, it was possible to test for temporal changes (within-subject treatment effects) while controlling for variability among sites (between-subject effects). Before analysis, data were examined for normality and homogeneity of variance, and no substantial difficulties were encountered. All repeated measures analyses met the assumption of sphericity (Moser et al. 1990) and, therefore, univariate results were used (actually, both univariate and multivariate results led to the same conclusions in all cases). Separate analyses were performed for each pair of the three time periods so that both

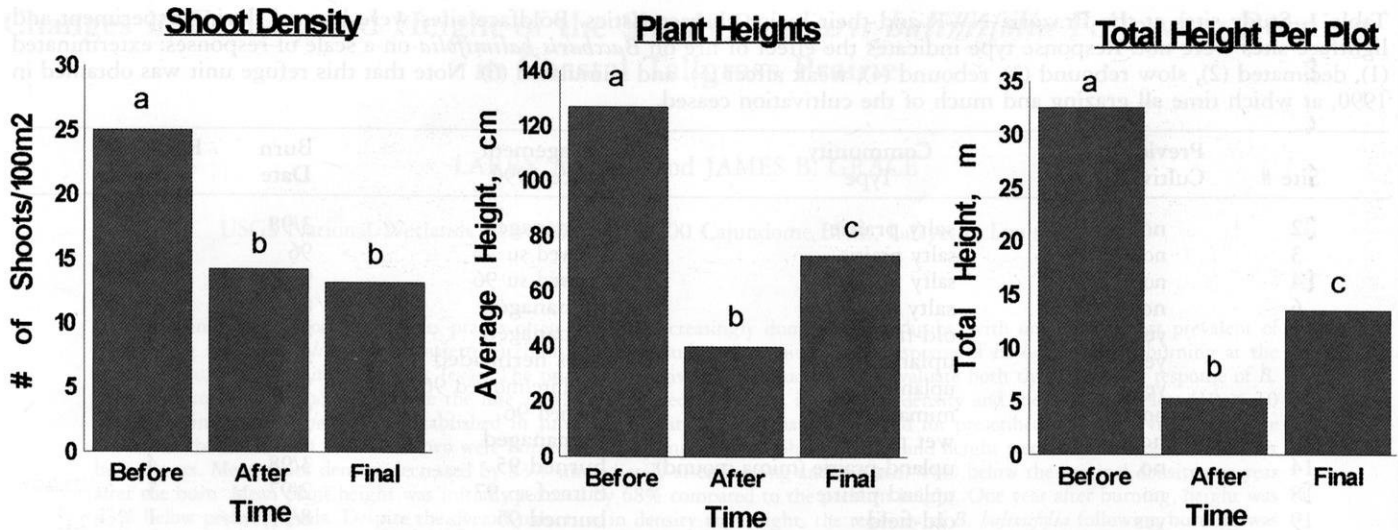


Fig. 1. Growth of *Baccharis halimifolia* in burned plots over duration of study. Bars labeled a, b, and c are significantly different from one another ($P < 0.05$).

individual time intervals and the total experiment could be evaluated.

The eight sites that had been burned prior to the study were also examined for change over time. Because data were not collected before the burns at these sites and because of the different burn times and site histories, only a limited interpretation of these data could be made.

The overall mortality and recovery of *B. halimifolia* after fire were based on the difference between prefire data and final data. To describe the qualitative responses of *B. halimifolia* to fires, each plot was classified as fitting one of the following patterns: exterminated, decimated, slow rebound, rebound, weak effect, stimulated.

RESULTS

The upper coastal prairie of Texas received below average rainfall in 1997 and 1998, and a ban on prescribed fire was in effect much of that time. Despite this, nine sites were able to be burned in the summer of 1997 before the ban was put in place, and two were burned in the spring of 1998 after the fire ban was lifted.

Field observations revealed several things about the response of *B. halimifolia* to fire. First, the burns observed in this study resulted in nearly complete topkill of *B. halimifolia* plants in the great majority of cases. Of the 11 prescribed burns, in only one case was there substantial resprouting from original stems, which appeared to be associated with a low-intensity fire. In all other cases, post-fire resprouting was largely confined to basal resprouts regardless of pre-fire plant size. Second, while root sprouting was observed on occasion, individual plants appeared to remain distinct and clearly identifiable in most cases. The single exception to this statement was observed at a monitoring site not included in this study that had been mechanically cut previously. At this site, the density of *B. halimifolia* was so great that individuals were not identifiable. The post-fire distinctness of individuals in *B. halimifolia* was in sharp contrast to our observations on certain other woody species such as *Myrica cerifera* L. (wax myrtle). For *M. cerifera*, patterns of resprouting following fire made it impossible to distinguish individuals consistently. Third, resprouting by *B. halimifolia* after fire occurred very rapidly. In many cases, new sprouts could be clearly recognized as early as 2–3 weeks following fire. Fourth, the great majority of post-fire *B. halimifolia* plants measured were individuals present before

the fires. However, excavations outside of the sample plots revealed that at least some of the post-fire increase in plant density over time may have resulted from seed germination. Because it is not possible to distinguish seedlings from root sprouts without destructive sampling, it is not known for certain how often establishment from seed took place in this study.

For the 11 sites burned during the study, the average pre-fire density of *B. halimifolia* plants was approximately 25 per 100 m² (Fig. 1). Average densities at individual sites ranged from a low of 5.5 to a high of 61.5 plants per m². Repeated measures analysis of variance indicated significant changes in density over time ($P < 0.01$). Following fire, average density declined by 43%, with no significant recovery by the end of the study. Individual sites, however, showed a range of patterns of responses to burning (Fig. 2, Table 1). For example, at site 24, burning initially reduced density by more than 69%. However, by the end of the study, plant density had recovered to 72% of the pre-burn density. In contrast, at site 13, density was reduced by 90% following fire, and there was no indication of recovery during the period of observation.

Average pre-fire plant heights were greater than 120 cm, with the averages for individual sites ranging from 56 to 178 cm (Fig. 1). Following fire, most *B. halimifolia* plants were observed to be top killed, thus initially, their post-fire heights were essentially zero. However, at the time of first measurement following fire, which ranged from 3 to 10 weeks following the burn, average height was approximately 40 cm, a 68% reduction ($P < 0.01$). On average, plants that survived the fire continued to regrow during the period of observation and at the end of the study had recovered to a height of approximately 70 cm.

One way of expressing the total abundance of *B. halimifolia* at a site is by summing the heights of all measured plants. Initial total height per plot averaged greater than 3,000 cm (Fig. 1). The abundance of *B. halimifolia* at individual sites varied between 247 and 8,396 cm, reflecting both variations in density and individual heights. On average, total height per site was reduced to about 500 cm (84%) following fire and recovered to nearly 1,500 cm by the end of the study ($P < 0.01$). As with the other parameters, the dynamics of total height varied substantially among sites (Fig. 2). At site 24, total height recovered to within nearly 75% of the pre-fire value by the end of the study. At site 13, however, *B. halimifolia*

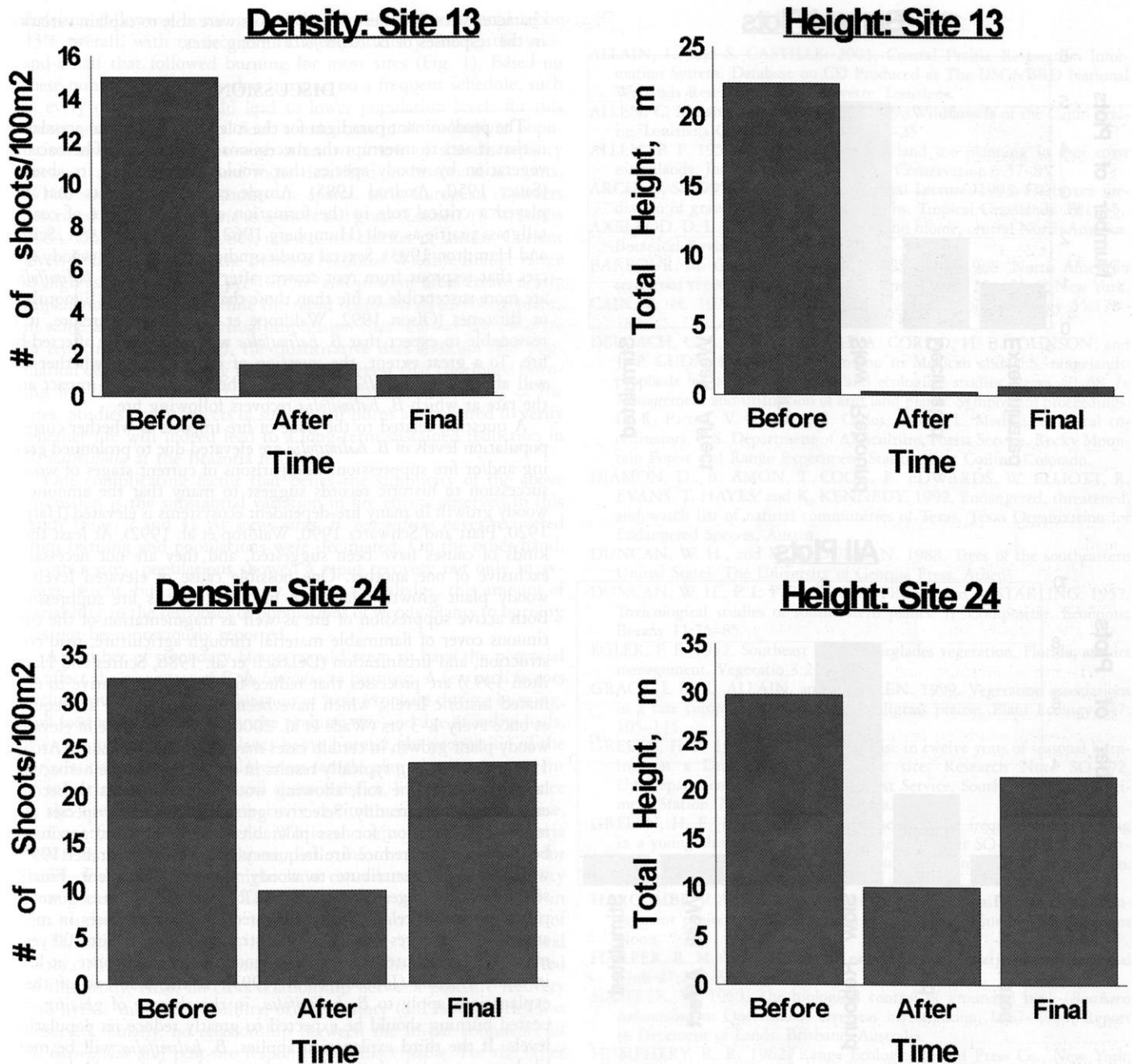


Fig. 2. Examples of the range of responses among sites. Total height and density at site 24 are significantly reduced after fire but recover significantly by the final assessment. Site 13 demonstrates an extreme response, with most plants dying after being burned.

was nearly eliminated, with substantial mortality and with little regrowth by surviving plants.

To simplify discussion of responses to burning, temporal responses in density, average height, and total height for individual sites were used to classify *B. halimifolia* responses into different categories (Fig. 3). Ultimately, total height was used as the most synthetic parameter for making determinations of the overall effects of fire. This analysis included not only the 11 sites burned during the period of observation but was also extended to include plots burned prior to the study. At one site, *B. halimifolia* was essentially eliminated by burn-

ing (based on its abundance at the end of the observation period) and was classified as exterminated. Where density and total height were greatly reduced relative to pre-fire levels, it was classified as decimated. At some sites, recovery of populations following fire was observed to be very slow, which was described as a slow rebound pattern. This was in contrast to those sites where recovery of density and regrowth following fire was relatively rapid, which was classified as a rebound pattern. One site examined appeared to be hardly affected due to little mortality and extremely rapid regrowth rates. Finally, one site showed a rapid increase in plant density as well as

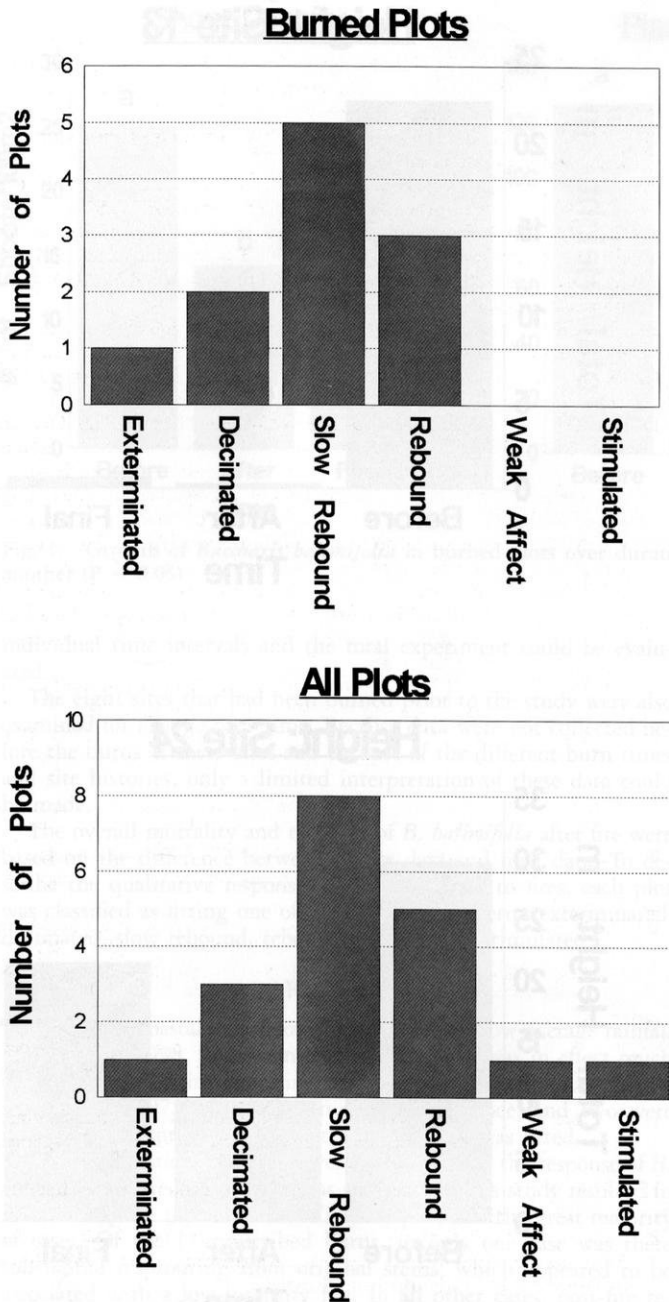


Fig. 3. Overall effect of fire on *Baccharis balimifolia*. The first graph shows only those plots burned during our study. The second graph represents the range of responses at all plots.

rapid regrowth following fire and was classified as being stimulated by the fire. Examination of the frequency distributions of both (1) the 11 plots burned during the study and (2) the total set of plots examined revealed that the most common response to burning was a slow rebound (Fig. 3). A more rapid rebound was also common and overall; plots that showed signs of recovery were in the majority.

Because of the high degree of variability among sites in the patterns of response by *B. balimifolia*, analyses were conducted to determine whether response patterns correlated with either prairie type (upland, salty, or oldfield), with total preburn height, or with soil

characteristics. Neither of these factors were able to explain variation in the responses of *B. balimifolia* among sites.

DISCUSSION

The predominant paradigm for the role of fire in natural grasslands is that it acts to interrupt the successional replacement of herbaceous vegetation by woody species that would take place in its absence (Sauer 1950, Axelrod 1985). Ample evidence suggests that fire played a critical role in the formation and maintenance of coastal tallgrass prairie as well (Humphrey 1962, Smeins et al. 1991, Scifres and Hamilton 1993). Several studies indicated that those woody species that resprout from root crowns after fire, such as *B. balimifolia*, are more susceptible to fire than those that resprout from lignotubers or rhizomes (Olson 1992, Waldrop et al. 1992). Therefore, it is reasonable to expect that *B. balimifolia* will be adversely affected by fire. To a great extent, the question of interest is not whether fire will affect *B. balimifolia* but instead, the magnitude of impact and the rate at which *B. balimifolia* recovers following fire.

A question related to the issue of fire impacts is whether current population levels of *B. balimifolia* are elevated due to prolonged grazing and/or fire suppression. Comparisons of current stages of woody succession to historic records suggest to many that the amount of woody growth in many fire-dependent ecosystems is elevated (Harper 1920, Platt and Schwartz 1990, Waldrop et al. 1992). At least three kinds of causes have been suggested, and they are not necessarily exclusive of one another. One possible cause of elevated levels of woody plant growth relative to historic levels is fire suppression. Both active suppression of fire as well as fragmentation of the continuous cover of flammable material through agriculture, road construction, and urbanization (DeLoach et al. 1986, Scifres and Hamilton 1993) are processes that reduce fire frequency relative to estimated historic levels, which have been estimated to be as frequent as once every 1–3 yrs (Wade et al. 2000). A second cause of elevated woody plant growth in certain cases may be livestock grazing (Archer 1995). Overgrazing typically results in disturbance of the herbaceous layer as well as the soil, allowing woody plants species to become established more readily. Selective grazing of palatable species also reduces competition for less palatable species. Further, grazing is believed to often reduce fire frequency and intensity (Archer 1995), which can also contribute to woody plant establishment. Finally, some authors suggested a third possible cause of increased woody plant abundance relative to historic records, that increases in mean annual temperatures and CO₂ concentrations over the past 100 years may have contributed to a shift in woody plant dominance, at least in some systems (Johnson et al. 1993). If the first two of these explanations apply to *B. balimifolia*, in the absence of grazing, repeated burning should be expected to greatly reduce its population levels. If the third explanation applies, *B. balimifolia* will be more likely to retain a high population density, though frequent burning might still reduce its abundance.

Several authors have found prescribed fire to have less of an effect than expected on woody plant densities in several southern ecosystems (Olson 1992, Waldrop et al. 1992, Olson and Platt 1995). Some of the recent failures of prescribed fire to control woody plant growth may be associated with the use of dormant-season burning, though limited impacts of growing-season burns have also been reported. In this study, all fires conducted in areas containing *B. balimifolia* were conducted during the growing season. Because of the generally greater effects of growing-season burns compared to dormant-season burns, we interpret the results reported in this paper as representing some of the more extreme effects that fire can have on *B. balimifolia*.

In this study, there was a substantial decrease in *B. balimifolia*

densities following burning. Initial mortality was estimated to be 43% overall, with no recovery in average density during the year-and-a-half that followed burning for most sites (Fig. 1). Based on these numbers, it appears that burning on a frequent schedule, such as every other year, would lead to lower population levels for this component of the system. Such a reduction in *B. halimifolia* population levels is consistent with what we know of the discrepancy between current levels and those described in historical accounts. While such historical accounts are sparse, early European explorers described the coastal prairie as a sea of tall grass (Lockett 1874, Inglis 1964, Ohlendorf et al. 1980), not a dense thicket of shrubs. Current levels of *B. halimifolia* at the Brazoria National Wildlife Refuge range as high as over 60 plants per 100 m² and in some areas create nearly impenetrable thickets. While the rapid regrowth of surviving plants in some areas gives the visual impression that fire was not effective in reducing *B. halimifolia*, the quantitative data indicate that population densities are being reduced and suggest that continued burning may have a substantial effect on *B. halimifolia* at many of the sites. Studies on the effects of subsequent burns are required to verify whether fire will indeed lead to a long-term sustained reduction in *B. halimifolia* at the Brazoria refuge.

One complicating factor that belies the simplicity of the above discussion is the substantial variation in fire effects observed in this study (Figs. 2 and 3). At some sites, *B. halimifolia* never recovered from burning and populations were decimated. On the other hand, at other sites, populations showed a rapid recovery not only in average height, but also in density. To our knowledge, this amount of variability in the responses of populations of woody plants to burning has not been previously reported.

A number of secondary factors would seem to have the potential to affect the responses of *B. halimifolia* to burning. A few such factors include the intensity and duration of heat exposure during burning, fuel load and characteristics, the preburn size and age of individuals, the physiological state of plants being burned, the proportion of the population made up of male versus female plants, moisture content of soil at time of burning, soil characteristics, history of disturbance at the site, preexisting competitive environment, herbivory/disease, and postfire rainfall patterns. While the site history for Brazoria NWR is reasonably well-known, little information is available for many of the factors that might have contributed to the variability among sites in this study. The great majority of fires conducted in this study were sufficiently intense to result in complete topkill of *B. halimifolia* plants. Thus, if variation in fire intensity is a critical factor, it is operating at a more subtle level than could be detected in this study. Also, no clear relationship between post-fire recovery and hydric influences, salinity, or site history (old field/prairie) was observed. Finally, no relationship between the initial abundance of *B. halimifolia* and post-fire responses was discernable. For the other factors mentioned above, we can only say that we were not able to detect any apparent relationships, though this does not necessarily rule out their importance. In sum, this unexplained variability in response to burning at various sites suggests the need for studies in which experimental control over both fire and plant characteristics, as well as other factors, can be obtained.

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Defining Landscape Vision to Monitor and Manage Prescribed Fire at Badlands National Park, South Dakota

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The National Park Service recognizes fire as a vital ecosystem process and has directed parks to reintroduce fire to fire-dependent landscapes. In 1999, Badlands National Park began work on a new fire management plan to implement a landscape level prescribed fire program. To direct this plan, the park took a critical look at the changes that fire may make in the composition, distribution, and structure of important vegetation communities. A multi-disciplinary team approach was used to 1) determine three monitoring types and 2) define the desired landscape vision for each with goals and measurable objectives. A monitoring type is a combination of the vegetative community and the proposed fire treatment. Three types were selected based on an analysis of the communities defined in the park's vegetation map and management priorities: western wheatgrass alliance, introduced grassland complex, and a compilation of vegetation classes defined as woody draw. Factors taken into consideration in defining the landscape vision for each type were: fire history, fire ecology, species response, spatial scale and distribution, habitat values, distribution of exotic species, opportunities for visitor understanding, age-class distribution, structural complexity, and periodicity of prescribed fire.

INDEX DESCRIPTORS: prescribed fire, fire management, vegetation monitoring, Badlands National Park.

Badlands National Park, located in southwestern South Dakota, consists of nearly 100,000 ha (244,000 a) of sharply eroded buttes, pinnacles and spires blended with the largest, protected mixed-grass prairie in the United States. The 25,900 ha (64,000 a) designated wilderness in the park is the site of the reintroduction of two endangered prairie species: the swift fox, (*Vulpes velox*) and the black-footed ferret (*Mustela nigripes*). In the last three decades, North American bison (*Bison bison*) and Rocky Mountain bighorn sheep (*Ovis canadensis*) have also been re-established in the park. In addition to re-establishing native species, the park also seeks to re-establish or perpetuate natural processes, and one of the most fundamental processes to the park's prairie ecosystem is fire.

With large tracts of continuous, fine fuels, frequent periods of hot, dry weather, and recurrent lightning, the mixed-grass prairie in and around the park represents a classic grassland fire regime. Frequent, low-intensity surface fires with a return interval of 1 to 25 years typify this ecosystem (Pyne 1982) as exemplified in the composition of plant and animal species. Species diversity can be directly related to fire return interval and the randomness of the fire mosaic often determines species location and dispersal (Collins and Gibson 1990).

The earliest notations of fire in this ecosystem were detailed in the accounts of explorers, trappers and settlers whose records indicate a high occurrence of both natural and anthropogenic ignited fire (Higgins 1986). Fire, drought, herbivory, erosion and flooding are forces that define mixed-grass prairie in Badlands.

Over the last two decades, the park's fire management plan has undergone several revisions to adapt to the evolving science of fire ecology and changes in agency policy. The most recent iteration of

the fire management plan is currently in development. This plan will guide the use of prescribed fire at Badlands National Park for the next 15 years, and the current draft plans for over 19,630 ha (48,500 a) to be burned in 27 separate burn units. The resource management goals related to the prescribed fire program at Badlands National Park are:

- Shift vegetation composition in natural areas from less desirable exotic plant species (Japanese brome (*Bromus japonicus* Thunb. ex Murr.), smooth brome (*Bromus inermis* Leyss.), Kentucky bluegrass (*Poa pratensis* L.), crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.), and Canada thistle (*Cirsium arvense* (L.) Scop) to more favorable, native plant species.
- Promote hardwood regeneration, especially in woody draw areas of the park. Most, if not all, of these areas are decadent or remain dormant, and as a result, nutritional quality and productivity have declined. Without the rejuvenating effects of fire, these communities may continue to deteriorate, and the value to wildlife may also decline.
- Restore or gain the mosaic pattern of different plant communities associated with post-fire succession.
- Rehabilitate areas that have been planted or established with non-native grasses, primarily roadsides, pullouts, and other disturbed sites.
- Manage grasslands to increase suitable habitat for butterfly species that are listed on the South Dakota natural heritage list [e.g. regal fritillary (*Speyeria idalia*) and tawny crescent (*Phyciodes batesii*)].
- Improve the nutritional quality and palatability of native grasses, shrubs, and trees for use by ungulate species in the park.
- Maintain distribution of wildlife/range use throughout the park by burning large enough areas so American bison, bighorn sheep,

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Table 1. Plant community or cover class in hectares and acres expressed as percentages of the total landscape of Badlands National Park, South Dakota with reference to suitability of type for burning and woody draw inclusion.

Plant Community/Cover Class	Map Unit	Hectares	Percentage	Burnable?	Woody Draw?
Western Wheatgrass Alliance	16	35,715	36.6	Y	N
Blue Grama	18	3,291	3.4	Y	N
Introduced Grassland	17	2,064	2.1	Y	N
Little Bluestem-Grama-Threadleaf Sedge	15	2,051	2.1	Y	N
Silver Sagebrush/Western Wheatgrass	31	1,541	1.6	Y	N
Three-leaved Sumac/Threadleaf Sedge	35	751	0.8	Y	Y
Silver Sagebrush/Prairie Sandreed	32	599	0.6	Y	N
Western Wheatgrass-Green Needlegrass	19	599	0.6	Y	N
Soapweed Yucca/Prairie Sandreed	21	525	0.5	Y	N
Western Snowberry	37	452	0.5	Y	Y
Croplands	52	268	0.3	Y	N
Emergent Wetland	14	239	0.2	Y	N
Green Ash-(American Elm)/Chokecherry	42	188	0.2	Y	Y
Chokecherry-(American Plum)	34	184	0.2	Y	Y
Switchgrass	12	179	0.2	Y	Y
Ponderosa Pine/Rocky Mountain Juniper	43	141	0.1	Y	N
Rabbitbrush	33	7	0.0	Y	N
Silver Buffaloberry	25	7	0.0	Y	Y
<i>Burnable subtotal</i>		48,811	50.0		
Badlands Sparse Vegetation Complex	2	44,400	45.5	N	N
Prairie Dog Town Community	1	1,964	2.0	N	N
Juniper/Littleseed Ricegrass	44	1,061	1.1	N	N
Streams and Canals	55	899	0.9	N	N
Transportation, Communications, Utilities	51	185	0.2	N	N
Eastern Cottonwood	41	53	0.1	N	N
Reservoirs	56	50	0.1	N	N
Urban/Cropland/Pasture	52	36	0.0	N	N
Other Agricultural Land	54	28	0.0	N	N
Rivers-Perennial	50	21	0.0	N	N
Beaches and Sandy Areas	57	13	0.0	N	N
Strip Mines, Quarries and Gravel	59	12	0.0	N	N
Greasewood/Western Wheatgrass	39	5	0.0	N	N
Sandbar Willow Temporarily Flooded	38	5	0.0	N	N
Seeded Mixed Grass Prairie	54	0	0.0	N	N
<i>Unburnable subtotal</i>		48,733	50.0		

and both white-tailed and mule deer (*Odocoileus virginianus* and *O. hemionus*) do not become unnaturally concentrated.

- Restore fire as a critical component of ecosystem processes such as nutrient cycling.

To help guide the development of the prescribed fire program and to evaluate whether the resource objectives are being met, we needed to re-evaluate monitoring types. A monitoring type is a combination of the vegetative community and the proposed fire treatment. The existing monitoring types had been pieced together over a few years, were selected opportunistically based on the composition of the burn units, and did not include a landscape vision or integration with other monitoring types.

Over the winter of 2000, the lead fire monitor of the Northern Great Plains Fire Monitoring program, Kara Paintner, and the staff of Badlands National Park worked together to revise the park's primary monitoring types and develop a landscape vision for each monitoring type with goals and measurable objectives. Participants in this process included people with expertise in plant ecology, wildlife biology, park management, and fire operations. Over a series of brain-

storming meetings and follow-up discussions, the team was able to focus on three meaningful monitoring types that we believe will enable us to determine if we are meeting our overall fire management goals over the next 15 years.

SELECTION OF MONITORING TYPES

The park's recently released vegetation map (Von Loh et al. 1999) was used as a starting point to determine the most meaningful monitoring types. First, 32 map classes were divided into cover types that could burn and those that would not burn due to the lack of fuels (i.e., rivers, beaches, badlands sparse, prairie dog complex), lack of continuity between fuels [greasewood (*Sarcobatus vermiculatus* (Hook.) Torr), sandbar willow (*Salix exigua* Nutt.)], or high soil moistures [eastern cottonwood (*Populus deltoides* Bartr. ex Marsh)]. A map class is a clustering of similar map units within a vegetative community and/or land use. Of the 32 map classes, 17 map classes were determined to be burnable, accounting for about 50% of the park's acreage. Subsequent discussions focused on the "burnable" map classes (Table 1).

The acreage of each burnable map class was considered. Western wheatgrass (*Agropyron spicatum* Pursh) alliance accounted for 35,715 ha (88,252 acres) or 36.6% of the park's land area. Furthermore, this map class is distributed throughout the park. Due to the sheer abundance and obvious importance to the park's grassland ecosystem, western wheatgrass alliance was selected as a monitoring type. The rest of the burnable map classes ranged from 3.4% to 0.1% of the park's total area. Clearly, another criteria besides abundance was needed to select additional monitoring types.

Each burnable map class was considered in relation to management objectives with a focus on the role of fire in achieving those objectives. As do most prairie ecosystems, Badlands battles invasive plant species. Due to past land management practices, cool-season exotic grasses are well-established in some areas. Furthermore, there is a large body of research related to the use of prescribed fire to reduce or control cool-season exotic grasses, and this is one of the primary objectives of the prescribed fire program (Wright and Bailey 1980). Based on these criteria, the introduced grassland vegetation map class was selected as a monitoring type.

The ecological roles of the remaining 15 burnable map classes were considered. As the Badlands landscape is dominated by barren badlands and prairie, the pockets of woody vegetation are geographically rare and often provide rich wildlife habitat. Five map classes were grouped based on common woody draw species. They were three-leaved sumac (*Rhus trilobata* Nutt.), snowberry (*Symphoricarpos occidentalis* Hook.), green ash (*Fraxinus pennsylvanica* Marsh.), chokecherry (*Prunus americana* Marsh), and buffaloberry [*Shepherdia argentea* (Pursh) Nutt.]. This group covers 1,582 ha (3,909 a) or 3.2% of the park. Due to the importance of this community to the park's wildlife and the scattered distribution throughout the park, woody draw was selected as a third monitoring type.

DEVELOPING A LANDSCAPE VISION FOR EACH MONITORING TYPE

First, consideration was given to what the park's grasslands should look like in the future. The team agreed that exotic species, particularly cool-season grasses, should be reduced, and the natural diversity of associated native species should be preserved. Native forbs should be increased, and certain plant species should be increased for the habitat value provided to target wildlife species. The role of the park in the science of plant ecology was considered, and it was determined that the park should provide a laboratory to improve knowledge of fire effects on both plant and wildlife communities.

Next, the ecological characteristics of each monitoring type were considered. Each community was described based on pattern, process, structure, space, time, and function. The role of fire in each community was then identified, considering fire history, fire ecology, and the proposed periodicity of prescribed fire. Finally, each monitoring type was analyzed in its relation to the park's landscape and park's purpose, considering spatial scale and distribution, habitat values, distribution of exotic species, opportunities for visitor understanding, age-class distribution, and structural complexity. Each monitoring type was then fully described, and measurable goals and objectives were defined. Shortened versions of these types follow; full descriptions and/or sampling methods are in the monitoring plan, an appendix to the fire management plan.

MONITORING TYPES

Detailed descriptions of each of the three monitoring types follow as examples of the completed process. Each description is presented in a standard format so they are easily compared and contrasted. They start with a physical and biological description of the vegetation community based on information from the new vegetation map

and soil survey. A landscape vision statement that describes long-term management direction follows. The burn prescription includes a detailed description of the season and/or plant phenology of when burning should occur and the weather and fire behavior parameters for the fire treatment. The monitoring variables in order of importance identify the key components for meeting landscape objectives. These are also the variables used to look at minimum plot number calculations in power analysis. This is followed by two sets of objectives: prescribed fire project objectives define burn success over time and fire monitoring objectives define the accuracy and precision of monitoring variables.

WESTERN WHEATGRASS ALLIANCE

Physical Description

This community occurs in a wide variety of habitats through the park. Sites are generally flat to moderately steep in slope and occur on all aspects. Associations of the type occupy clay, silt, loam and sandy soils of flats, swales, drainages, hills and slopes (Von Loh et al. 1999). Elevations range from 730–1220 m (2,400 to 4,000 ft). Soils are clayey, silty, claypan, and badlands overflow. Soil types are: Blackpipe clay loam, Blackpipe-Norrest complex, Blackpipe-Wortman complex, Cedarpass silty clay loam, Cedarpass-Denby complex, Cedarpass-Interior-Badlands, Interior-Cedarpass-Denby (USDA-SCS, 1987).

Biological Description

Stands of this type have moderate to complete herbaceous cover between 40–100%. Western wheatgrass is strongly dominant in ungrazed stands; less so in stands subjected to annual grazing by livestock. Species dominance can vary locally within a stand depending on soils and use factors (Von Loh et al. 1999). Dominant graminoids are western wheatgrass, blue grama [*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths], and green needlegrass [*Nassella viridula* (Trin.) Barkworth]. Shrubs are plains prickly pear [*Opuntia polyacantha* Haw.), three-leaved sumac, sand sage (*Artemisia frigida* Willd.), and silver sagebrush (*A. cana* Pursh). Forbs include: heath aster (*Aster ericoides* L.), yarrow (*Achillea millefolium* L.), and Missouri goldenrod (*Solidago missouriensis* Nutt.).

Landscape Vision

Western wheatgrass mixed-grass prairie is believed to be the pre-settlement vegetation for the area (Kuchler 1964). The exact composition of the communities before settlement is unknown. The fire return intervals reported vary from as short as 5 yrs in level to gently rolling topography to 15–30 yrs in more broken topography at Scotts Bluff National Monument, Nebraska (Wendtland and Dodd 1992).

The community, when maintained by fire, would have reduced numbers of exotic species, particularly cool-season grasses. The natural diversity of associated native species would be preserved or increased. There would be short-term (2–4 yrs post burn) increase in native forbs, especially milkweed (*Asclepias* sp. L.) and other target species for butterflies. With continued burning we will improve knowledge of fire effects in this community. The community would have 25–50% of the area burned within the last 5 yrs depending on topography, with a mosaic of different aged stands across the type.

Burn Prescription

This prairie will be burned between April until green-up, or late July through a season ending event in the fall. Head, flanking, and backing fire will be used as needed to meet burn objectives.

Fire Prescription Elements

- Relative Humidity: 25–55%
- Dry Bulb: 0–30°C (32–85°F)
- Fuel loading: 0.67–1.12 kg/m² (3–5 tons per acre)
- Live Fuel Moisture: NA
- 1-hour Time Lag Fuel Moisture: 6–14%
- 10-hour Time Lag Fuel Moisture: 8–15%
- 100-hour Time Lag Fuel Moisture: 10–30%
- Average Flame Length: 0.12–.45 m (0.4–1.5 ft)
- Average Rate of Spread: 0–5 km/hr (0–3 mph)
- Average Mid-flame winds: 0–32 km/hr (0–20 mph)

Monitoring Variables (in order of importance)

1. Native Grass Relative Cover
2. Exotic Grass Relative Cover
3. Native Forb Relative Cover

Prescribed Fire Project Objectives

Immediate Post Burn

1. Burn 60–80% of the burnable project area

Two Years Post Burn

1. Reduce relative cover of non-native grasses by 20 to 30%
2. Increase relative cover of native grasses by 10 to 25%
3. Increase relative cover of native forbs by 30 to 40%

Fire Monitoring Objectives

1. Install enough plots to be 80% confident that the relative cover for native perennial grasses, non-native grasses, and native forbs is within 25% of the true population mean
2. Install enough plots to be 80% confident that the average density of all brush species is within 25% of the true population mean

INTRODUCED GRASSLAND

Physical Description

Many of these sites are associated with disturbances such as roadsides, abandoned farm fields and areas that were interseeded with exotic grasses to 'improve' the range for grazing. Areas with high disturbance include corridors along the park access road and facilities, abandoned agricultural fields along the northern boundary and Sheep Mountain Table, and in seedings on Cuny and Stronghold Tables. These areas are characterized by level to hilly badlands crossed by grassy drains, isolated buttes and lowland terraces. Historically, these areas supported western wheatgrass mixed prairie (Von Loh et al. 1999). All aspects are acceptable; slopes can range from 0–45%; elevations range from 730–1220 m (2,400 to 4,000 ft). Soils are clayey, silty, claypan, and badlands overflow. Soil types are: Blackpipe clay loam, Blackpipe-Norrest complex, Blackpipe-Wortman complex, Cedarpass silty clay loam, Cedarpass-Denby complex, Cedarpass-Interior-Badlands, Interior-Cedarpass-Denby (USDA-SCS 1987).

Biological Description

Stands typically have moderate herbaceous cover, ranging from 40–90% and very dense litter over the ground surface. Areas tend to be dominated by one exotic grass species, often planted. The dominant grass could be smooth brome, crested wheatgrass, or Kentucky bluegrass. Other exotic species associated with these areas include: Japanese brome, cheatgrass (*B. tectorum* L.), alfalfa (*Medicago sativa* L.), yellow sweet clover [*Melilotus officinalis* (L.) Lam], and common mullein (*Verbascum thapsus* L.). At the edge and occasionally

interspersed are western wheatgrass, needle and thread (*Stipa comata* Trin. & Rupr.), and green needlegrass. Very few native forbs or shrubs are seen in this type (Von Loh et al. 1999).

Landscape Vision

The sites, although mostly exotic cool-season grasses now, would have been western wheatgrass mixed-grass prairies prior to European habitation of the area (Kuchler 1964). The exact composition of the communities before settlement is unknown. The fire return intervals reported vary from as short as 5 yrs in level to gently rolling topography to 15–30 yrs in more broken topography at Scotts Bluff National Monument, Nebraska (Wendtland and Dodd 1992). It is believed that the fire return interval in these areas would have been relatively short.

The community when maintained by fire would have reduced numbers of exotic species, particularly cool-season grasses. Repeated spring burning will check the spread of these grasses into native prairie. The number of native grass and forb species will increase, increasing the biodiversity of these areas. The burns are highly visible due to the proximity of disturbed sites to visitor use areas. This provides an opportunity for visitor understanding and education about prescribed fire and exotic species control. The park would like these areas to ultimately be returned to mostly native plant communities and eventually have no need for this monitoring type.

Burn Prescription

This prairie will be burned when the plant phenology is between green-up and heading-out of the seed. The burn will preferably be conducted with the seed head is being developed, a stage called the 'boot.' Backing fire will be used to generate longer resident times (more heat) and do the most damage to the undesired species.

Fire Prescription Elements (see western wheatgrass alliance)

Monitoring Variables (in order of importance)

1. Exotic Grass Relative Cover
2. Species that is being targeted Relative Cover
3. Native Grass Relative Cover

Prescribed Fire Project Objectives

Immediate Post Burn

1. Burn 80–100% of the burnable project area

One Year Post Burn

1. Reduce relative cover of non-native grasses by 30 to 50%
2. Increase relative cover of native grasses by 10 to 25%
3. Increase relative cover of native forbs by 10 to 25%
4. No change in wildlife-auto collisions due to increased forage in roadside burn areas

Five Year Post Burn

1. Maintain 30–50% reduction of non-native grass relative cover
2. Maintain increase of relative cover of native grass and forbs

Fire Monitoring Objectives

1. Install enough plots to be 80% confident that the relative cover for non-native grasses is within 20% of the true population mean
2. Install enough plots to be 80% confident that the relative cover of the target grass is within 25% of the true population mean
3. Install enough plots to be 80% confident that the relative cover of native grass and forbs is within 25% of the true population mean

WOODY DRAW

Physical Description

These draws occur in less-steep mesic draws, small perennial drainages, and at the bases of sandhills (Von Loh et al. 1999). The vegetation normally occurs on the draw bottoms and lower sideslopes (Warner 1993) as shrubby to wooded draws. All aspects are acceptable, slopes can range from 0–60%, elevation 730–1220 m (2,400 to 4,000 ft). Soils are clayey, silty, claypan, and badlands overflow. Soil types are: Interior-Cedarpass-Denby, Interior loam, channeled, Midway silty clay loam, and Orella-Badlands (USDA-SCS 1987).

Biological Description

This habitat type encompasses several different plant communities as described in Van Loh et al. (1999). Vegetation communities grouped into this monitoring type are based on a Green Ash/Elm Woody Draw and the surrounding communities. Associated edge communities in drier areas are Rocky Mountain Juniper (*Juniperus scopulorum* Sarg)/Little-seed Ricegrass [*Oryzopsis micrantha* (Trin. & Rupr.) Thurb.] and Woodland and Ponderosa Pine (*Pinus ponderosa* P. & C. Lawson)/Rocky Mountain Juniper Woodland. Shrublands that occur at draw sides and heads include chokecherry, western snowberry, and ill-scented sumac. Stands typically have closed canopies dominated by green ash and some American elm (*Ulmus americana* L.). Cottonwood and peachleaf willow (*Salix amygdaloides* Anders.) will be present if there is a spring or seep. Shrubs are sparse in the understory, but form dense communities along the edge. Shrubs include chokecherry, western snowberry, ill-scented sumac and poison ivy (*Toxicodendron rydbergii* L.). The herbaceous component includes Kentucky bluegrass, western wheatgrass, and big bluestem (*Andropogon gerardii* Vitman) (Von Loh et al. 1999).

Landscape Vision

Woody draws are believed to be part of the pre-settlement landscape for the area (Boldt et al. 1978). The exact composition of the vegetation within those communities before settlement is unknown. Deciduous trees are reported to be no older than 50 yrs and juniper no older than 100 (Warner 1993). The fire return intervals of 15–30 yrs were estimated for more broken topography at Scotts Bluff National Monument, Nebraska (Wendtland and Dodd 1992). This return interval would have interacted with long-term wet and dry periods for the area. The edges of these draws would have been impacted by the return intervals and fire frequencies of the surrounding prairie. The more mesic areas of the draws would have only been likely to burn in dry periods.

When maintained by fire, the community will have a mosaic of different age classes within a watershed. Browse for ungulates will increase. Sheltering cover will remain within 25% of current levels. Siberian elm (*Ulmus pumila*), Canada thistle and associated exotic species related to homestead establishment and occupation will be reduced. Eighty percent of structural complexity will be maintained. The length of the edge habitat will be increased or maintained within 10% of current levels.

Burn Prescription

These draws will be burned in concert with the surrounding prairie. Typically, the prairie will be burned between April until green-up, or late July through a season ending event in the fall. Firing methods and unit preparation will be used to exclude fire from some draws. Head, flanking, and, backing fire will be used as needed to meet burn objectives.

Fire Prescription Elements (see western wheatgrass alliance)

Monitoring Variables (in order of importance)

1. Overstory Tree Density
2. Density of specific browse species as directed by the wildlife biologist
3. Total Herbaceous Relative Cover

Prescribed Fire Project Objectives

Immediate Post Burn

1. Reduce total down and dead woody fuel load by 20–60%

One Year Post Burn

1. Increase density of desired browse species by 30 to 50%

Two Year Post Burn

1. Maintain or increase edge length

Five Year Post Burn

1. Limit overstory tree mortality to no more than 25%

Fire Monitoring Objectives

1. Install enough plots to be 80% confident that the density of overstory trees is within 20% of the true population mean
2. Install enough plots to be 80% confident that the density of targeted browse species is within 25% of the true population mean
3. Install enough plots to be 80% confident that the relative cover of herbaceous plants is within 25% of the true population mean

CONCLUSIONS

The final monitoring plan is still in draft along with the fire management plan, so the true test of this process is yet to come. Finding realistic objectives is an iterative process; it may be likely that we were optimistic in our expectations of the post fire response in some areas. In addition, future monitoring results may indicate the need to add or split current types. In all cases, the thought process alone helped park managers define and refine their goals for use of prescribed fire as a management tool.

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A Fungal Endophyte in Canada Wild Rye: Studies on Its Occurrence, Detection and Elimination

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Canada wild rye (*Elymus canadensis* L.) is a native tallgrass species that, unlike the dominant grasses big bluestem (*Andropogon gerardii* Vitman), indiagrass (*Sorghastrum nutans* L.) and switchgrass (*Panicum virgatum* L.), is a cool season bunchgrass. Thus, this species contributes to the lifeform diversity of tallgrass prairies and may be a key factor in providing wildlife habitat and forage in early spring and late fall, when C₄ species are dormant. Like many other cool season grass species, Canada wild rye harbors a fungal endophyte, growing intercellularly in the above ground plant tissues. The plant-fungal relationship has been well-studied in grasses of agronomic importance such as species of fescue (*Festuca* L.) and ryegrass (*Lolium* L.). In some cases, the relationship seems to be a mutualism, with the fungus enhancing growth and producing compounds that deter herbivores. Little is known about the ecological costs and benefits of endophytic fungal infection in Canada wild rye. This study is designed to 1) quantify the extent of infection in Canada wild rye throughout the tallgrass prairie region, 2) detect the fungus in plant tissue and with isolation techniques and 3) experimentally eliminate the fungus from living plant tissue to obtain material to compare infected to non-infected plants. Our results suggest that 1) fungal infection rates are much higher than anticipated, 2) the fungal appearance in plants and in culture agrees with previous descriptions and 3) simple seed treatment and fungicide techniques that have been effective in agronomic species do not always eliminate the fungus from Canada wild rye tissue.

Index Descriptors: fungal endophyte, *Neotyphodium*, *Elymus canadensis*, propiconazole, Canada wild rye.

Fungal endophytes grow in intercellular spaces of the above ground tissues of many grasses. The fungi are often asymptomatic and occur in all grass subfamilies and in most of the large grass genera (Clay 1990). Extensive research has been done on the effects of the fungus on plant growth and palatability in agronomically important species of fescue and ryegrass, particularly tall fescue (*Festuca arundinacea* Schreb.) and perennial ryegrass (*Lolium perenne* L.). In these species, endophyte infected (E+) plants cause disorders in grazing cattle and decrease rates of insect herbivory (Bacon et al. 1977, Funk et al. 1983, Clay et al. 1985). In addition, some evidence suggests that E+ plants have higher drought tolerance than E- plants (Arachevaleta et al. 1989). Results from studies on fescue and ryegrass have led to the general conclusion that endophyte infection may represent a mutualism between grasses and fungi.

Grass-endophyte associations may be viewed more broadly as a continuum of interactions, ranging from parasitic to mutualistic relationships. White (1988) divided grass-endophyte associations into three types depending on their mode of transmission and degree of positive effects on the plant. In Type 1 associations, the fungal hyphae form stromata (an external mass of hyphae) that collar the developing flowering culms and effectively stop seed head development, a disease known as choke. Fungal reproduction in Type 1 association is either vertical, hyphae spreading with seeds, or horizontal, spread by spores from plant to plant. This association could be considered parasitic because it involves negative effects on plant reproduction. In Type 3 associations, the fungal hyphae do not develop outside the plant, stromata are never formed and fungal reproduction is exclusively vertical. Type 3 associations tend to involve positive effects such as herbivore deterrence and enhanced plant growth. This is the type of association that is characteristic of most species of the well-studied genera *Festuca* and *Lolium*. In Type 2 associations, stromata

are formed on 1–10% of the plants, even though 50–75% of the plants may harbor the fungus in intercellular spaces and both vertical and horizontal fungal reproduction may take place. The endophyte in Canada wild rye is known to occasionally form stromata on the plant, and frequently hyphae are present in the seed. Thus, this fungal-plant relationship may be categorized as a Type 2 association (White 1988).

Canada wild rye is a native, cool-season bunchgrass, abundant in tall and mixed-grass prairies. A study of herbarium specimens suggested that fungi are present in about 60% of the Canada wild rye individuals in North America (White 1987). Based on field observations, it is thought that 1–10% of these individual plants develop the stromata and thus have the potential for sexual reproduction, while in the remaining infected individuals, the fungus reproduces vegetatively by growing into the seed (White and Bultman 1987). The identity and taxonomic status of the fungal endophyte in Canada wild rye, as with endophytes in other hosts, has recently undergone a revised interpretation. The fungus is similar to *Epichloë typhina* (Ascomycetes), but because the sexual structures are seldom observed, the endophyte fungus has been placed, along with other related grass endophytes, into the genus *Neotyphodium* (Glenn et al. 1996). Because the taxonomy of these fungi is the subject of ongoing research, we will refer to the Canada wild rye endophyte as "*Neotyphodium*" throughout the paper and will treat *Neotyphodium* as a functional group that may include one or more species in Canada wild rye. We expect that more published observations on the morphology of the fungal endophyte of Canada wild rye will further the taxonomic studies and complement genetic approaches to those studies.

Little is known about the effects of *Neotyphodium* on Canada wild rye and whether or not E+ plants have some advantages in terms of herbivore deterrence and growth increases over E- plants. Before

Table 1. Sites where germplasm of *Elymus canadensis* was collected and screened for the presence of a fungal endophyte.

Location	Nearest Town	Longitude/Latitude	Endophyte in Seed	Endophyte in Plant
Loda Cemetery	Loda, IL	88.05W/40.32N	+	+
McLean Right of Way	Danvers, IL	89.10W/40.32N	+	+
Beach Cemetery	Rockford, IL	89.08W/42.08N	+	+
Holt County	Mound City, MO	95.12W/40.08N	+	+
Atchison County Roadside	Rockport, MO	95.29W/40.25N	+	+
Iron Horse	Hayfield, MN	92.50W/43.55N	+	+
Compass	Worthington, MN	95.40W/43.40N	+	+
Willow Township Cemetery	Charter Oak, IA	95.36W/42.04N	+	+
Sioux City	Sioux City, IA	96.20W/42.28N	+	+
Narodni Hrbitor Cemetery	Touhy, NE	96.52W/41.08N	+	+
Nine Mile Prairie	Lincoln, NE	96.50W/40.45N	+	+
Vinton Ranch	Mullen, NE	101.20W/41.70N	+	+
Konza Prairie	Manhattan, KS	96.50W/39.20N	+	+
OKCS-38	Beaver, OK	100.29W/36.36N	+	+
OKCS-30	Elk City, OK	99.40W/35.15N	+	+
OKCS-26	Mangum, OK	99.46W/35.03N	+	+
OKCS-29	Erick, OK	99.54W/35.05N	+	+
OKCS-23	Snyder, OK	98.55W/34.48N	+	+
OKCS-20	Snyder, OK	98.55W/34.48N	+	+
OKCS-16	Waurika, OK	98.05W/34.09N	+	+
OKCS-7	Lone Grove, OK	97.16W/34.10N	+	+
OKCS-19	Lawton, OK	98.30W/34.27N	+	+
OKCS-9, OKCS-40	Frederick, OK	98.52W/34.16N	+	+
TXCS-13	Graham, TX	98.41W/33.11N	+	-
TXCS-28	Wellington, TX	100.27W/34.50N	+	+
TXCS-27	Childress, TX	100.17W/34.43N	+	+
TXCS-17	Paducah, TX	100.17W/34.15N	+	+
TXCS-20	Guthrie, TX	100.14W/33.34N	+	+
TXCS-22	Crowell, TX	99.35W/33.48N	+	+
TXCS-23	Henrietta, TX	98.01W/33.38N	+	+
TXCS-15	Electra, TX	98.54W/33.58N	+	+
TXCS-11	Montague, TX	97.39W/33.39N	+	+
TXCS-30	Montague, TX	97.37W/33.45N	+	-
TXCS-12	Nocona, TX	97.57W/33.31N	+	-
TXCS-24	Dallas, TX	97.07W/32.56N	+	-

this issue can be studied, reliable means of detecting the endophytic fungi and experimentally ridding some plant tissue of this fungus are needed. The literature is dominated by studies on species of fescue and ryegrass in agronomic settings, where the cultivation of a small number of cultivars may restrict the type of endophyte and the range of grass responses. The techniques and results published for ryegrass and fescue may not be applicable to Canada wild rye. In this paper, we: 1) report efforts to document the occurrence of endophytic fungi in natural populations of Canada wild rye in the Midwest and southern Great Plains, 2) provide evidence to confirm previous observations on the appearance of the endophytic fungi in the plant and in culture and 3) explore means of experimentally ridding plants of fungi.

METHODS

Collection of Plant Tissue for Endophyte Screening

Seeds and tillers of Canada wild rye were collected from 36 sites throughout the Midwest and southern Great Plains. Collections of plant tissue came from Nebraska, Kansas, Minnesota, Iowa, Missouri, Illinois, Oklahoma, and Texas (Table 1). In some cases, the seed was propagated in a greenhouse and plants were transplanted into com-

mon gardens before we collected tissue for endophyte screening. See Vinton et. al. (2001) for details of tissue collection and site location. All tissues were refrigerated until endophyte screening could take place.

Endophyte Detection Methods

We used three means of detecting the fungi. Two methods were used for detecting hyphae in the tiller tissues, and one method was used for testing for hyphae in the seeds. For the tillers, we used an epidermal peel technique (Bacon and White 1994) and a commercially available immunoblot assay specific for *Neotyphodium* in fescue (Agrinostics Ltd. Co.; 1501 Hickory Hill Drive; Watkinsville, GA 30677). We tested for hyphae in seeds by using a direct microscopy technique (Larch et al. 1987).

The epidermal peel method involved removing the outer leaf of the tiller and taking an epidermal peel of the sheath tissue from inside of the leaf blade. The peel was made using a razor blade to slice gently along a cut edge of sheath tissue, while viewing the tissue under a dissecting microscope, until a sufficient length of upper epidermis could be separated from the rest of the tissue. In some cases, particularly with older plants, the epidermis did not yield

easily into large enough peels. In these cases, sheath tissue was soaked in a 10% potassium hydroxide (KOH) solution overnight to soften and clear the tissue. Leaf sheath tissue from younger plants was generally not treated with KOH. The epidermal peel was placed on a microscope slide and stained in aniline blue solution (0.325 g aniline blue, 100 ml water, 50 ml 85% lactic acid). The slide was heated for 1 min on the "low" heat setting of a laboratory hot plate, and the excess dye was removed using a tissue and distilled water. We placed a cover slip over the stained peel and viewed it under a light microscope. Hyphae were visible at 100x, and we confirmed their presence at 400x. The fungal endophyte was present in leaf sheaths as straight and sometimes wavy hyphae typically much longer than an individual plant cell and never appearing to invade the plant cells.

The monoclonal antibody (MAB) test kit involved placing a cross section (2–3 mm) of the tiller on top of a nitrocellulose membrane. This membrane held 100 tiller cross sections. Thus, the MAB kit poses some advantages over the epidermal peel technique described above in that many samples can be screened in a relatively short time. The tillers on the nitrocellulose membrane were placed in an extraction buffer and incubated at 4°C overnight. The membrane was blocked and monoclonal antibodies were added. We then washed the membrane, and a second antibody was added, which resulted in a "stacking" of antibodies. The membrane was washed again, and a protein with an alkaline phosphatase enzyme conjugate was added to complete the stacking process. Then the protein complex was washed off, a chromogen solution was added, and presence of the *Neotyphodium* protein on the membrane was indicated by development of a faint pink color. We noted the importance of having known E- samples, which may leave a faint shadow on the membrane, to insure that the degree of color development could be accurately related to endophyte presence.

We tested the seeds using a direct microscopy technique that involved soaking the seeds in 5% NaOH solution for 8 h to soften the seed. The NaOH solution was removed by placing a mesh screen over the beaker and rinsing the seeds with tap water for 20 min. We then deglumed the seeds and placed them in an aniline blue solution (0.325 g aniline blue, 100 ml water, 50 ml 85% lactic acid). The seeds and solution were warmed on a hot plate for approximately 1.5 min for the aleurone layer of the seed to become adequately stained. We rinsed the seeds with distilled water, placed a seed on the microscope slide, and squashed the seed with a cover slip before examination with a light microscope. We considered a seed E+ when dense mats of hyphae could be seen within the aleurone layer of the seed.

Plating Techniques

We plated the tissue from a random sample of 80 seeds and 30 greenhouse-grown plants using techniques described in Bacon and White (1994). Seeds and 5 mm sections of tillers were placed in 1.25% Clorox® (NaOCl) and agitated on an orbital shaker for 5 min, at which time one-third of the tillers were removed from the solution and rinsed in sterile, deionized water. Using sterile forceps, we placed three tiller sections on each plate of potato dextrose agar (PDA). The remaining two-thirds of the tillers were agitated for another 5 min, and one third of this group was rinsed and three sections placed on each plate. The final one-third of tiller sections were disinfected another 5 min, rinsed and placed on plates. The plates were sealed with parafilm and incubated in the dark at 25°C.

The seeds were disinfected in a similar manner as the tiller sections, except all the seeds were agitated in the Clorox® solution for 15 min. The Clorox® solution was then poured off and the seeds were rinsed with sterile, deionized water for 5 min. The water was decanted and replaced with more sterile, deionized water in which

seeds were agitated for another 3–4 min. Using sterile forceps, we removed the seeds and placed four seeds in the PDA plates. The plates were sealed with parafilm and incubated with the tiller plates. Plates were observed once/day, and transfers took place as necessary. When the relatively slow-growing, fungal endophyte developed on the agar, we took samples to view with the light microscope.

Elimination Techniques

To produce E- plants, we followed protocols developed for *Neotyphodium* in tall fescue (Nicholas Hill, Dept. of Crop and Soil Science, Univ. Georgia, Athens, GA 30602; Belesky et al. 1989) and treated E+ Canada wild rye seedlings with a systemic fungicide. To eliminate the endophyte in seed, we treated E+ Canada wild rye seeds with an incubation method subjecting the seeds to heat and humidity (Andrew Hopkins, Noble Foundation Inc., Ardmore, OK 73401; Harvey et al. 1982, Latch and Christensen 1982, Siegel et al. 1984). Both procedures are described below.

We transplanted E+ seedlings into 3.8 × 21 cm conetainers (Stuewe and Sons, Inc., 2290 SE Kiger Island Drive, Corvallis, OR 97333), one seedling per container, after germinating seeds in flats. Conetainers are tube-shaped vessels with drainage holes and fit into racks similar to test-tube holders. Each rack holds 98 conetainers. We submersed the entire rack of conetainers into a vat containing a Banner fungicide (14.3% propiconazole) solution of 1.20 ml/L water (0.16 oz/gal). We let the conetainers soak in the fungicide solution until the soil at the tops of the conetainers was moist, approximately 8 h. We did not water the plants the prior day, so the soil in the conetainers was relatively dry and readily soaked up the fungicide solution. This method provided a much more rapid way to expose many plants simultaneously to systemic fungicide than those methods described in Bacon and White (1994) and in De Battista et al. (1990). The fungicide-drenching procedure was repeated with the racks of conetainers containing seedlings once a week for 4 weeks. A rack of control tillers were treated in the same way, except no fungicide was added to the solution. After the final fungicide application, we removed the plants from the conetainers and placed them into 15 cm diameter × 17 cm diameter (1 gal) plastic pots. We observed some growth distortions on fungicide-treated plants and measured tiller length and width of treated vs. non-treated plants. A two-sample T test assuming unequal variances was used to detect differences in leaf width and length of fungicide-treated versus non-treated plants.

To avoid confusion of living and dead hyphae in fungicide-treated tillers, we allowed the treated plants to grow for approximately 4 months and produce daughter tillers, which were used to screen for endophytes. The plants were grown under 23.8°C day and 12.8°C night temperatures and artificial lighting for 10 h/day. The fungal hyphae were not expected to be present in the daughter tillers if the fungicide technique was successful.

To screen for hyphae in the daughter tillers of the fungicide-treated and non-treated plants, we used two of the detection methods previously described. First, we used the MAB test kit on 50 daughter tillers of the fungicide-treated plants and 50 tillers from the non-treated plants. We also used the epidermal peel technique on the sheath tissue of the fungicide-treated daughter tillers to screen for hyphae.

To eliminate fungal endophytes in seed, we placed 20 g of E+ seeds in a warm, moist environment to kill the endophyte in the seed. The seeds were kept at 37–38°C in an incubator containing a pan of water to increase the humidity. The seeds were left in the oven for a period of 3 weeks before we screened them for endophytes. The seeds were screened for the endophyte using the direct microscopy technique, previously described, on softened seed tissue. We

Table 2. Results of PDA plate cultures that contained non-treated Canada wild rye tillers (NT CWR-T), fungicide-treated Canada wild rye tillers (FT CWR-T), non-treated Canada wild rye seeds (NT CWR-S), and incubated-treated Canada wild rye seeds (IT CWR-S).

Tissue Type	n	Plate Appearance			
		Endo-phyte (%)	Other Fungi (%)	Bacteria (%)	Dead (%)
NT CWR-T	15	40	0	60	0
FT CWR-T	15	34	13	40	13
NT CWR-S	40	13	87	0	0
IT CWR-S	40	0	100	0	0



Fig. 1. Colonies of fungal endophyte of *Elymus canadensis*, isolated from tillers.

also germinated 30 of these seeds and used the epidermal peel technique to detect hyphae in the sheath tissue of the tillers grown from the treated seeds.

RESULTS AND DISCUSSION

Extent of Infection in Midwest and Southern Great Plains

We used direct microscopy techniques on sheath tissue and seeds to detect the fungi, *Neotyphodium*, in Canada wild rye from 36 sites throughout the Midwest and southern Great Plains (Vinton et al. 2001). The endophytic fungus was found in seed from all sites and in plants from all but four sites (Table 1). The fungus appears more widespread than earlier reports indicated; whether or not this widespread fungus affects plant growth or palatability is not known.

Plating

We attempted to isolate the endophyte from 15 fungicide-treated Canada wild rye tillers (FT CWR-T), 15 non-treated Canada wild rye tillers (NT CWR-T), 40 incubated-treated Canada wild rye seeds (IT CWR-S), and 40 non-treated Canada wild rye seeds (NT CWR-

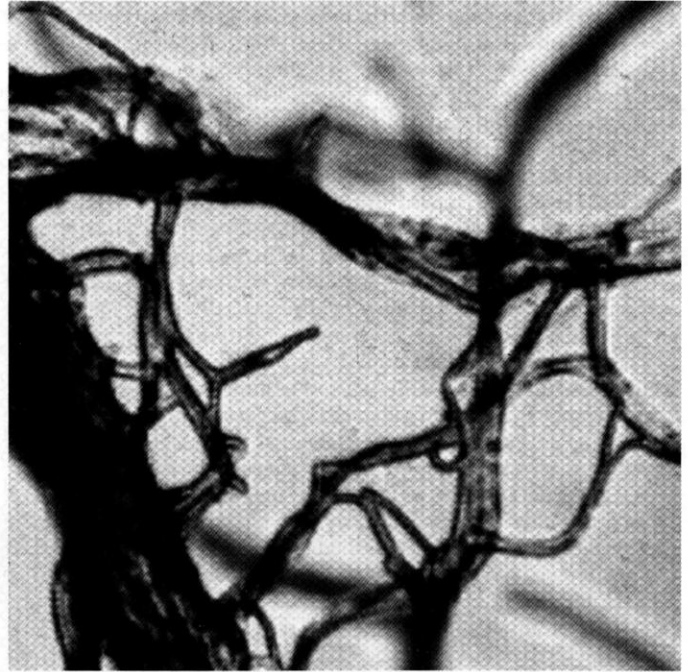


Fig. 2. Hyphae and phialides of plated specimens of the fungal endophyte in *Elymus canadensis*.

S) (Table 2). Endophytic fungi grew from both treated and non-treated tillers. The non-treated seed also resulted in some growth of the endophyte, while the incubated-treated seeds did not support the endophyte. In general, the tillers resulted in more certain appearance of the endophytic fungi than did the seed tissue (40% vs. 13%). Two weeks after the initial plating, endophytic fungal hyphae grew out the ends of the tiller sections so that the entire mass was dumbbell-shaped. Because the endophyte was slow growing, other, more rapid growing fungi threatened to overgrow the plates. Thus, swabs of the putative endophytic fungus were cultured on fresh plates once per week. After 2–3 weeks, the fungal colony was 2–3 cm in diameter with white, cottony mycelium above the agar and brown when viewed from the bottom of the plate (Fig. 1). The rate of growth (first appearance of endophyte at 2 weeks after culture was started) and colony appearance (white, cottony) matched those of White and Morgan-Jones (1987) who cultured the endophytic fungi of Canada wild rye.

The seeds (especially the incubated-treated seeds) had a high rate of non-endophyte fungal growth (Table 2) during the plating process, and some of the tillers seemed to have dead tissue on the plates. Other studies have found that seeds require a more thorough decontamination protocol than tillers to eliminate surface bacteria and fungi (Marshall et al. 1999). For fresh tillers, however, a longer soaking period in the Clorox® solution seems to result in early death of the tissue. Given the drawbacks involved with surface sterilization and growth of foreign bacteria and fungi on the plates, the plating technique is not appropriate for accurately screening tillers and seeds for the presence of endophytic fungi.

After the endophyte appeared on the PDA plates, we examined mycelium microscopically. Hyphae were septate, and conidia were produced after 1–2 weeks of growth. We observed solitary phialides (Fig. 2), which in some cases appeared to have a basal septa.

Table 3. Mean leaf width and tiller height of fungicide-treated and non-treated Canada wild rye plants. Standard errors are shown in parentheses. The second leaf on the oldest tiller of twenty-five fungicide- and non-treated plants was measured. Leaf width was measured at 1 mm from the ligule. Tiller height was measured from base of oldest tiller to highest node. For both parameters a T-test was conducted for treated vs. non-treated plants. Superscripts indicate differences at $P \leq 0.005$.

Treatment	n	Leaf Width (mm)	Tiller Height (cm)
Fungicide-treated	25	7.6 (1.4) ^a	7.7 (1.6) ^b
Non-treated	25	6.6 (1.3) ^b	19.2 (7.2) ^a

Elimination of Endophytic Fungi from E+ Plants

The epidermal peel detection method of the daughter tillers of fungicide-treated plants showed the endophyte still present in 19 out of 19 tested plants. The results from the MAB test kit gave E+ results for all 50 of the non-treated tillers and for the 50 fungicide-treated tillers. When the seeds that had been incubated to eliminate the fungus were examined, we found that this elimination technique was also ineffective. Endophytic fungal hyphae were visible in the aleurone layer of 17 out of 17 seeds tested, using the direct microscopy technique. The result was similar for the epidermal peels taken from the plants grown from incubated seeds, with 30 out of 30 plants still being endophyte infected.

The 100% infection rate in plants treated either by fungicide or incubation demonstrated that these elimination techniques were not effective in killing the endophyte. In contrast, numerous studies have shown that propiconazole significantly reduced the occurrence of endophytes in perennial ryegrass seedlings (Harvey et al. 1982, Wilson et al. 1995) and seeds (Harvey et al. 1982, Latch and Christensen 1982, Siegel et al. 1984). The protocols developed for endophytes in agronomic grasses may not be applicable to the endophytes present in native prairie grasses.

Canada wild rye seedlings that had been submerged in the propiconazole solutions had altered leaf width and tiller height (Table 3). The leaf width of the fungicide-treated plants was significantly wider ($P < 0.05$) than the non-treated plants (Table 3). The fungicide-treated plants also had significantly ($P < 0.05$) shorter tillers (Table 3) than the E+ Canada wild rye plants not treated with propiconazole. These responses were consistent with studies (Latch and Christensen 1982, Wilson et al. 1995) of propiconazole effects on perennial ryegrass.

The changes in leaf width and tiller height of the propiconazole-treated Canada wild rye suggested that the fungicide was absorbed by the plant. Furthermore, these growth distortions coincided with effects on plants in which the endophyte was eliminated in perennial ryegrass (Latch and Christensen 1982). Latch and Christensen (1988) reported that E+ perennial ryegrass could be treated for rust fungi with propiconazole at lower levels that would not cause phytotoxic symptoms, and that these levels did not kill the endophyte. Apparently, the propiconazole application rate used in this study was enough to cause phytotoxic symptoms but not high enough to kill the endophyte.

Conclusions

Our studies have shown that *Neotyphodium* is much more prevalent in natural populations of Canada wild rye than previous studies suggested (White 1987, Clay and Leuchtman 1989). The appearance of the fungi within tillers and on plates matched those of previous studies (White and Morgan-Jones 1987). The widespread nature of

the fungal infection in this species suggests that the association may be mutualistic (e.g. the fungi may be conferring enhanced drought resistance or herbivore resistance to plants), as has been found in tall fescue (Bacon et al. 1977, Funk et al. 1983, Clay et al. 1985, Arachevaleta et al. 1989). However, Saikkonen et al. (1999) found no evidence that endophytes confer grazing resistance in native Arizona fescue populations and suggest endophytes in natural populations may be important in increasing pathogen resistance and competitive ability of adult plants rather than in mediating interactions with herbivores (Saikkonen et al. 1998). In any case, managers of tallgrass prairie could use more information on endophytic fungi effects on Canada wild rye. Managers may be interested in planting Canada wild rye because it is a native tallgrass species that, unlike the dominant big bluestem (*Andropogon gerardii* Vitman), indiagrass (*Sorghastrum nutans* L.) and switchgrass (*Panicum virgatum* L.) is a C₃ (cool season) bunchgrass. This species contributes to the lifeform diversity of tallgrass prairies and may be a key factor in providing wildlife habitat and forage in early spring and late fall when C₄ species are dormant. However, managers need to know the consequences of planting endophyte-infected seed. For example, E+ plants may be avoided by grazers, yet be more productive under drought conditions than E- plants. Thus, the decision to plant E+ seeds may involve some advantages and disadvantages from a management viewpoint.

To examine the exact nature of the plant-fungal association in Canada wild rye, it will be necessary to produce endophyte-free plants, preferably from clones of endophyte-infected plants. Techniques used to successfully eliminate the fungus in species of fescue and ryegrass were not effective in Canada wild rye. Other recent studies on endophytes in natural grass populations (Schulthess and Faeth, 1998 and Saikkonen et al. 1998 and 1999) have also indicated that some generalizations and techniques that apply to the agronomic grasses do not apply to natural populations of native grasses. Clearly, more work is needed on native grasses to develop effective fungal endophyte elimination techniques and to clarify the ecological significance of this common plant-fungal association.

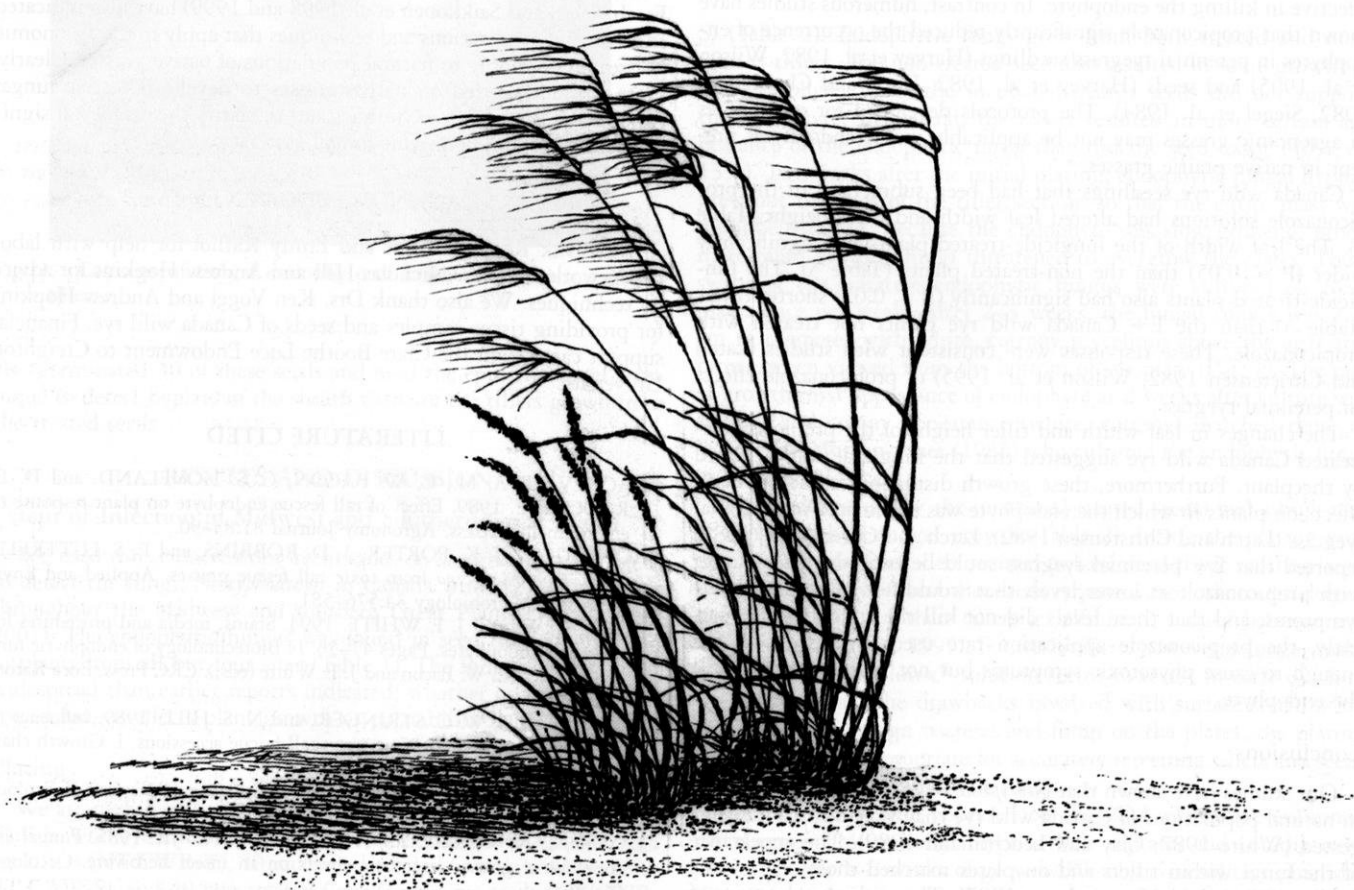
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Recovering Tallgrass Communities in Southern Ontario: An Ecosystem-based Recovery Plan and Implementation Progress

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Tallgrass prairie and oak savanna comprise some of the most endangered ecological communities in Canada. Found in Ontario and in southern Manitoba, less than 1% of the original extent remains nationally. In southern Ontario, 28 species associated with tallgrass communities are nationally listed as at risk of extirpation from Canada, and four species are known to have been extirpated. The main threat facing most of these species is habitat degradation and loss.

In 1997, World Wildlife Fund Canada and the Ontario Ministry of Natural Resources cooperated to develop a recovery plan for tallgrass communities in southern Ontario, which was one of the first ecosystem-based recovery plans to be completed in the country. The recovery plan lays out actions necessary for ecosystem recovery, including remnant securement and restoration work, community education, increased coordination and communication among conservationists, technology transfer, and applied research. The recovery plan called for the establishment of an organization to provide coordination and leadership. In response, Tallgrass Ontario, an association of volunteers, was set up to drive the implementation of the recovery plan. Two years after the recovery plan was developed, a number of successes can be reported. Tallgrass Ontario and its partners have instigated a number of cooperative projects, including an annual summer event series, a communications network, public education activities and products, remnant protection, tallgrass creation work, and practitioner workshops.

INDEX DESCRIPTORS: southern Ontario, recovery plan, Ontario Tallgrass Prairie and Savanna Association, Tallgrass Ontario.

Southern Ontario comprises a mere one-quarter of 1% of Canada's land mass, yet this region contains a large proportion of the species at risk of extinction in Canada. Southern Ontario contains Canada's share of the eastern deciduous forest. However, unknown to most, this region is also home to tallgrass prairie and savanna, referred to collectively as tallgrass communities.

In Canada, tallgrass communities are found in southern Manitoba, adjacent northwestern Ontario, and in southern Ontario. They are considered some of Canada's most endangered ecological communities; less than 1% of the original extent remains (World Wildlife Fund Canada 1989, Government of Canada 1991). In southern Ontario, tallgrass communities once covered approximately 1,000 km² in patches across an otherwise largely forested landscape (Fig. 1 in Rodger 1998). Now only 21 km², about 2%, remains (Bakowsky and Riley 1994), the balance lost largely to urbanization and agricultural use. While not large in area, tallgrass is part of Ontario's natural heritage and represents the northern edge of a globally imperiled ecosystem. As of November 2000, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) had listed a total of 364 species considered nationally at risk of extinction (COSEWIC 2000a, COSEWIC 2000b). Of these, 32 species, nine percent of species nationally at risk, are associated with tallgrass communities in southern Ontario, including the American badger (*Taxidea taxus jacksoni*), Henslow's sparrow (*Ammodramus henslowii*), blue racer snake (*Coluber constrictor foxii*), and small white lady's-slipper (*Cypripedium candidum*), all listed as endangered (COSEWIC 2000a, COSEWIC 2000b). Four of those 32 tallgrass-associated species are listed as extirpated from Canada: the Karner blue (*Lycaeides melissa*

samuelis) and frosted elfin (*Incisalia irus*) butterflies, greater prairie chicken (*Tympanuchus cupido*), and Illinois tick trefoil (*Desmodium illinoense*) (COSEWIC 2000a). Over 150 floral and faunal associates are considered provincially rare (Rodger 1998).

A RECOVERY PLAN FOR TALLGRASS COMMUNITIES

In 1997, World Wildlife Fund Canada (WWF) and the Ontario Ministry of Natural Resources (OMNR) joined forces to explore ideas for recovering species at risk in tallgrass communities. It soon became clear that the number one threat to most tallgrass species was habitat degradation and loss. Thus, recovering these species meant recovering tallgrass communities as a whole.

Over the next year, WWF and OMNR cooperated to produce *Tallgrass Communities of Southern Ontario: A Recovery Plan* (Rodger 1998), one of the first ecosystem-based recovery plans of its type in the country. The recovery plan (TRP) summarizes the state of tallgrass communities in southern Ontario and lays out the specific actions necessary to recover tallgrass across its range in southern Ontario. TRP is organized and guided by eight goal statements:

1. to improve communication, coordination and information-sharing among those involved in tallgrass community conservation;
2. to amass complete information regarding all tallgrass community remnants in southern Ontario;
3. to establish and expand a network of protected tallgrass community remnants;
4. to encourage protection of tallgrass remnants through sound management;
5. to encourage restoration and habitat creation initiatives where

- appropriate to enlarge existing remnants, make linkages and create new habitat;
- 6. to raise public awareness and appreciation of tallgrass communities;
- 7. to reduce significantly the number of tallgrass community species at risk; and
- 8. to encourage basic and applied research relevant to tallgrass community conservation.

The recommended action items range from developing a priority list of tallgrass remnants that require conservation action and encouraging conservation through various methods, including landowner stewardship and purchase and conservation easements, to encouraging habitat creation and developing a comprehensive campaign to raise public awareness. All actions are set into an ambitious five-year implementation schedule along with suggested key participants for each action item.

FROM PLAN TO ACTION: AN ASSOCIATION TO LEAD THE WAY

Once TRP was completed, the next important step was to develop an organized entity dedicated to guide, coordinate and spearhead plan implementation. To initiate this, WWF, OMNR and the Rural Lambton Stewardship Network, a county-based land stewardship initiative, called an organizational meeting. The result was the formation of the Ontario Tallgrass Prairie and Savanna Association, now known as Tallgrass Ontario, in early 1998. At its core is a small volunteer steering committee (approximately 10 people) made up of concerned individuals and representatives of agencies and community groups concerned with recovering Ontario's tallgrass heritage. Supporting this core is an increasing number of members and partner organizations who are actively working to accomplish the goals of TRP in their communities. Tallgrass Ontario's mission statement is "To achieve the identification, conservation, management and restoration of tallgrass prairie, savanna and related ecological communities in Ontario."

Tallgrass Ontario was envisioned as a hub connecting the activities of a wide range of groups and individuals. It has been set up to help people become more informed about tallgrass communities in the province; to encourage them to get involved in conservation and restoration work and to help them find the tools to do so; to facilitate project partnerships; and to share insights and information, all with the ultimate aim of achieving the goals set out in TRP.

RECOVERY PLAN IMPLEMENTATION: PROGRESS AND FUTURE PLANS

Tallgrass Ontario has made significant progress in the two years since its inception. A part-time paid coordinator supports the steering committee and operates the communications hub. The organization is active in raising public awareness and advocating greater participation in tallgrass research and restoration work. Quarterly newsletters and a web site (www.tallgrassontario.org) provide a good communications link. Tallgrass Ontario has hosted several educational events, including a prescribed burn workshop for restoration practitioners; it also helps profile local tallgrass-related events by advertising them collectively as an annual summer event series called "Prairie Summer." It is working toward providing an information clearinghouse and a technical support role to those interested in tallgrass conservation work. Currently, a series of fact sheets are being written, and two web-accessible databases are being developed for members to access frequently requested information. One database will list information about each known tallgrass conservation and restoration project in Ontario; the other will provide listings of use-

ful printed literature and other information resources relevant to tallgrass conservation in Ontario.

Tallgrass Ontario operates on a modest budget that provides for one part-time staff position and the materials and fees associated with its communications activities (approximately \$40,000 CDN/yr). Much of the substance of the project work, such as writing fact sheets, providing advice, leading tours and giving talks, is a volunteer effort by steering committee members and other partners. In addition to this operating budget, the organization receives grants from time to time to support specific activities. For example, with the help of a recent \$80,000 CDN grant from a Canadian private foundation, Tallgrass Ontario is set to launch the first phase of a landowner contact and stewardship initiative called Save Ontario Savannas (S.O.S.). It is hoped that this program will greatly increase the number of tallgrass remnants being restored and conserved by their owners.

The hands-on work of securing tallgrass remnants and tallgrass restoration is done not by Tallgrass Ontario itself, but through the organization's members and partners. While this work has been occurring in scattered areas for several decades, the last five years have brought a marked increase in activity. Efforts come from a variety of sectors, including naturalist and community groups, municipalities, OMNR, conservation authorities, schools, corporate citizens, and individuals. In the past year, for instance, the City of Windsor, Ontario announced its intention to purchase 56 ha of the Spring Garden Natural Area in the city, while the West Elgin Nature Club, a naturalist club in rural southern Ontario, secured an agreement with a rail company to lease and restore a 3 km stretch of rail line prairie. Both sites support numerous species rare to Ontario and are considered two of the best remnants in the province.

Work to restore and manage remnants on both public and private lands is increasing, and tallgrass restoration projects are starting up across southern Ontario. Another positive development is the increasing availability of local native seed due to a growing cottage industry and the development of one, non-profit large-scale seed nursery. The marked increase in both remnant management and creation projects has also led to an increasing demand for prescribed burn services. OMNR has, to date, been the main body undertaking prescribed burns for tallgrass restoration in southern Ontario. However, demand has outstripped capacity, and alternate delivery options are now being explored, such as the use of volunteers, including local fire departments, or the creation of private companies offering prescribed burn services.

There has been a large and continually growing demand for advice regarding various aspects of restoration projects, from choosing appropriate species and obtaining local seed to site preparation and post-planting management. While some high-quality literature is available (e.g., Morgan et al. 1995, Packard and Mutel 1997), until recently, there existed no comprehensive guide tailored to tallgrass restoration work in southern Ontario. To fulfill this need, Environment Canada has been working with several Tallgrass Ontario members and other restoration practitioners to produce the recently published *Planting the Seed: A Guide to Establishing Prairie and Meadow Communities in Southern Ontario* (Delaney et al. 2000).

A FUTURE FOR TALLGRASS IN SOUTHERN ONTARIO

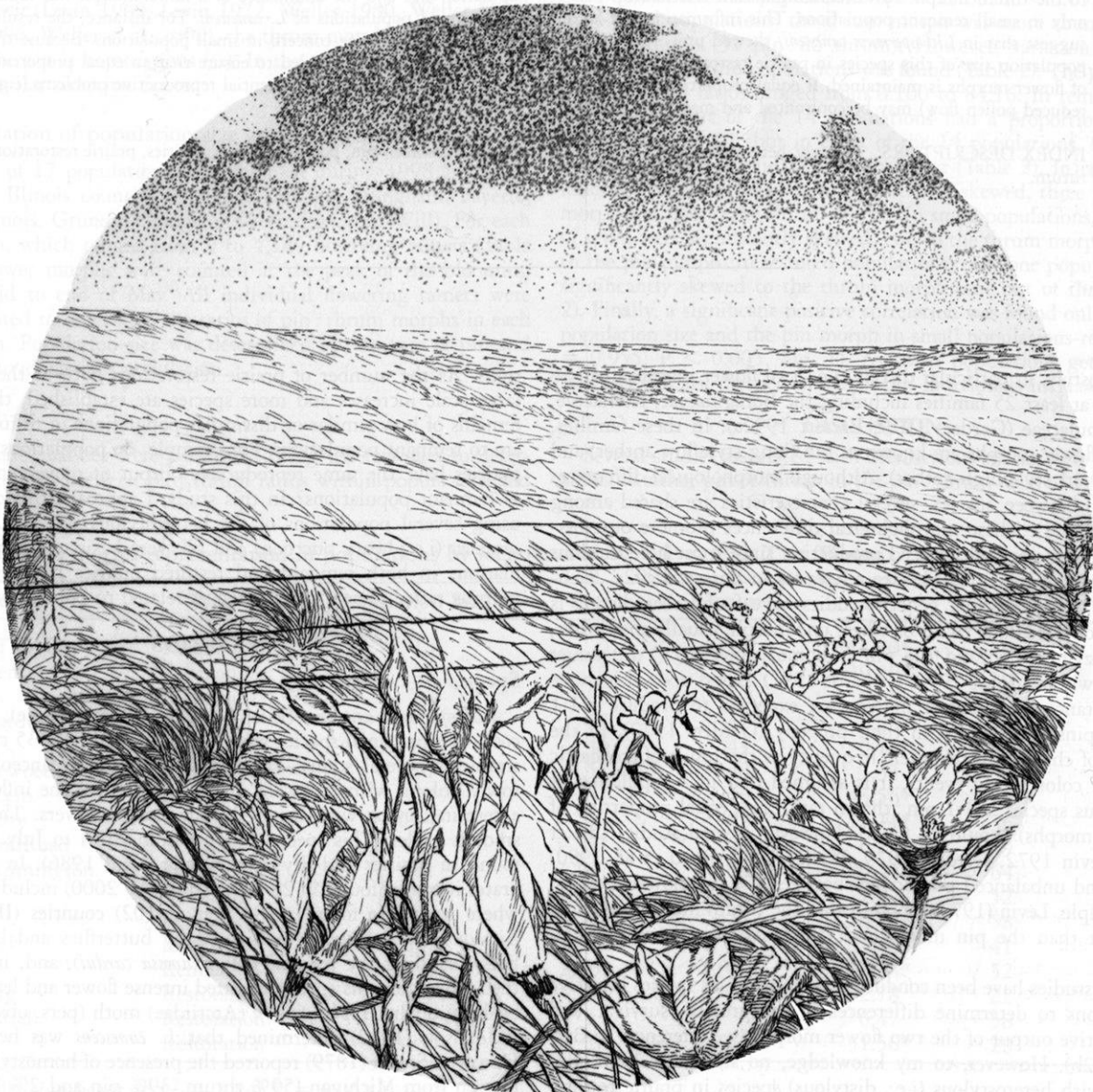
There is still much to be done to secure a healthy future for tallgrass communities in southern Ontario. However, a huge amount of progress has been made in the past few years, and the interest and activity continues to build. That healthy future is within our grasp, and all those involved in the efforts of Tallgrass Ontario will continue to reach toward it.

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What Can Happen to Heterostylous Species in Prairie Restorations? The Case of *Lithospermum canescens* (Boraginaceae)

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In distylous species, two flower morphs (pin and thrum) are found. The proportion of these flower morphs is predicted to be 1:1; however, several studies have found that this is not always the case. One flower morph is often more abundant than the other. Under these circumstances pollen flow may be reduced or biased, which could compromise the reproductive output of the species. In this study, I examined *Lithospermum canescens*, a distylous prairie species, to determine 1) whether its flower morphs occur in a 1:1 proportion in both restored and remnant populations; and 2) whether flower morph proportion is related to population size. Seventeen Illinois populations of *L. canescens* were studied. Significant differences in the proportion of flower morphs were found in some populations. Several of the remnant populations were skewed to the pin or thrum morph, while several of the restored populations were skewed to the thrum morph. However, a significant relationship between population size and the abundance of a flower morph was found only in small remnant populations. This information can be applied to restored populations of *L. canescens*. For instance, the results suggest that in *Lithospermum canescens*, skewed proportions in flower morphs are of extreme concern in small populations. Because the population size of this species in prairie restorations is small, particular attention may be needed to ensure that an equal proportion of flower morphs is maintained. If equal proportion of both flower morphs can not be achieved, potential reproductive problems (e.g., reduced pollen flow) may be confronted and may preclude restoration success.

INDEX DESCRIPTORS: Distyly, heterostyle, hoary puccoon, *Lithospermum canescens*, pin, population size, prairies, prairie restoration, thrum.

Heterostyly, in particular distyly (i.e., two flower morphs), can be found in at least 25 families including the Boraginaceae, Rubiaceae, and Primulaceae (Gardner 1979, Barrett 1992a). In these families, the two flower morphs are known as pin (long style/low anther) and thrum (short style/high anther). Although morphological differences are found between species, several characteristics are shared among them (Table 1). These morphological differences promote outcrossing, which is essential for seed production since most heterostylous species are self-incompatible (see references in Barrett 1992a, Richards 1997). In addition, genetic studies have found that distyly is based upon a diallelic factor *Ss* where one morph, usually the thrum, is heterozygous (*Ss*) and the pin is homozygous (*ss*) (Vuilleumier 1967, Lewis and Jones 1992, Richards 1997). Based upon this mode of inheritance, both flower morphs are expected to produce a 1:1 ratio of pins and thrums in their progeny (Gardner 1979). In the absence of changes in the allele frequency as the result of stochastic events or colonization events, it is assumed that in a population of a distylous species, a 1:1 pin : thrum ratio (i.e., equal proportion of the two morphs) should be found. However, several studies (Baker 1961, Levin 1972, Gardner 1979, Weller 1980, Boyd et al. 1990) have found unbalanced proportions between the two flower morphs. For example, Levin (1972) reported that the thrum morph was more abundant than the pin morph in *Lithospermum carolinense* populations.

Many studies have been conducted with distylous species in native populations to determine differences in the growth, survival, and reproductive output of the two flower morphs (see references in Barrett 1992b). However, to my knowledge, no study has been conducted with heterostylous (i.e., distylous) species in prairie restora-

tions. As the number of prairie restorations both at the small and large scale increases and more species are established, the question remains of how similar or dissimilar populations in restored prairies are to remnant populations. For example, do populations in restored prairies have the same reproductive output or movement of pollen as remnant populations? In this study, I approach this question by using several populations of the heterostylous species *Lithospermum canescens* (i.e., hoary puccoon) and ask very basic questions, do populations in both remnant and restored prairies have a 1:1 flower morphs ratio? If not, are differences related to population size?

METHODS

Species

Lithospermum canescens (Michx.) Lehm. (Boraginaceae), hoary puccoon, is a perennial species with a thick taproot, 12-35 cm tall with simple to several stems. The leaves are alternate lanceolate to narrowly oblong with canescent or sericeous hairs. The inflorescence is a terminal cyme with bright yellow-orange flowers. The fruit is a smooth nutlet. This species blooms from April to July and can be found in prairies and dry open woods (Kaul 1986). In the United States it can be found in 28 states (BONAP 2000) including Illinois, where it can be found in 83 (out of 102) counties (IPIN 2000). *Lithospermum canescens* is pollinated by butterflies and long-tongue bees including the painted lady (*Vanessa cardui*), and, in several of the study sites, this species endured intense flower and leaf herbivory by larva of the *Haplao reversa* (Arctiidae) moth (pers. obs.).

Johnson (1952) determined that *L. canescens* was heterostylous. However, Smith (1879) reported the presence of homostyly in a population from Michigan (59% thrum, 39% pin and 2% homostyly),

Table 1. Common characters in heterostylous species (from Richards 1997).

Character	Pin	Thrum
Style length	Long	Short
Stigma papilla length	Long	Short
Stylar cells	Long	Short
Anther position in tube	Low	High
Pollen size	Small	Large
Pollen number	Many	Few
Genetic control	Homozygous	Heterozygous

which to this day has been the only record suggesting trimorphism in *L. canescens*. Studies from Iowa and at the herbarium in the University of California, Berkeley, did not find trimorphism in *L. canescens* (Baker 1961). Also, in the Boraginaceae family it has been determined that for several members (Lewis and Jones 1992), including *L. carolinense* (Levin 1968, Levin 1972, Weller 1980, Weller 1985, McCall 1996, Weller et al. 2000), the thrum morph is heterozygous (Ss) and the pin is homozygous (ss). In the case of *L. canescens*, most likely a similar situation exists.

Determination of population size and flower morphs

A total of 17 populations were sampled during 1998 and 1999 in several Illinois counties (Douglas, DuPage, Effingham, Fayette, Ford, Iroquois, Grundy, Livingston, Vermilion, and Will). For each population, which ranged from 9 to 4,149 flowering ramets (Table 2), the flower morphs were counted at the peak of the blooming season, mid to end of May. All individual flowering ramets were hand-counted to determine the ratios of pin : thrum morphs in each population. Population size was determined by the sum of pin and thrum individuals in a population.

Data analysis

Chi-square analyses were performed using the raw data to determine differences between pin : thrum ratios within populations and

for the following comparisons: 1) complete data set, 2) only remnant populations (large and small), 3) remnant-large populations, 4) restored and remnant-small populations, 5) remnant-small populations, and 6) restored-small populations. Spearman correlations were used to test for a relationship between population size and the percentage of pin or thrum individuals. For these correlations, the data were grouped as above (1-6). Small populations were defined as having less than 100 individuals. Although this cutoff mark is arbitrary, several studies have shown that small populations (fewer than a 100 individuals) have lower fruit-set, seed set, seed germination rates, and quantity or quality of pollinator service (see references in Molano-Flores and Hendrix 1999). Normality was tested using normal probability plots. Population sizes were log transformed prior to statistical analyses. All statistical analyses were performed using Systat 7.0 (1997).

RESULTS

No significant variation in flower morph ratios was found in all comparisons (all χ^2 values ≤ 3.53 , $P > 0.05$, Table 3) with the exception of restored populations ($\chi^2 = 25.85$, $P < 0.05$, Table 3). In restored populations, the thrum morph was more abundant than the pin morph (31 pin : 86 thrum). However, variation in flower morph ratios within populations was found (Table 2). The percentage of pin : thrum ratios ranged from 0:100 to 84:16. In remnant populations, six out of the 14 populations had a proportion of pin : thrum close to 1:1, but in eight of the 14 populations, one flower morph was more abundant than the other (Table 2). In large populations, five out of seven were significantly skewed, three to the pin morph and two to the thrum morph. In small populations, three out of seven were significantly skewed, two to the thrum morph and one to the pin morph. In restored populations, only one population was significantly skewed to the thrum morph (one out of three) (Table 2). Finally, a significant positive correlation was found only between population size and the pin morph in small populations-remnant ($R = 0.955$, $P < 0.005$, Fig. 1). As small populations get closer to 100 individuals, the percentage of pin individuals increases.

DISCUSSION

Several studies associated with hetrostylous species have suggested a bias to either pin or thrum in the pin : thrum ratio of a population

Table 2. Flower morph representation in populations by location and type (P = Pin; T = Thrum).

Location	Type	Population Size	Pin	Thrum	χ^2	%P	%T
Hwy53/RTIDNR	Remnant	14	0	14	14.00*	0	100
Pearson Cem.	Remnant	39	0	39	39.00*	0	100
Loda Cem.	Remnant	62	30	32	0.06	48	52
Hwy53/Gardner	Remnant	68	27	41	2.88	40	60
29-1400	Remnant	85	44	41	0.11	52	48
12mPEdgewood	Remnant	91	51	40	1.33	56	44
Prospect Cem.	Remnant	97	81	16	43.56*	84	16
12mPFayette	Remnant	144	52	92	11.11*	36	64
Hwy53/HoffRoad	Remnant	179	87	92	0.14	49	51
Hwy53/Wilmington	Remnant	261	167	94	20.42*	64	36
English	Remnant	552	289	263	1.22	52	48
Belmont	Remnant	1,019	592	427	26.72*	58	42
Grant Creek	Remnant	3,022	1,251	1,771	89.48*	41	59
Sunbury	Remnant	4,149	2,162	1,987	7.38*	52	48
Schulenberg	Restoration	9	2	7	2.78	22	78
Doris Westfall	Restoration	19	11	8	0.47	58	42
Gardner	Restoration	89	18	71	31.56*	20	80

*Statistically significant at $\chi^2 = 3.84$, $P = 0.05$

Table 3. Flower morph representation by comparison.

Comparisons	Pin	Thrum	χ^2
All populations (remnants and restored)	4,864	5,035	2.95
Only remnant populations (large and small)	4,833	4,949	1.38
Remnant-large populations	4,600	4,726	1.70
Remnant and restored-small populations	264	309	3.53
Remnant-small populations	233	223	0.22
Restored-small populations	31	86	25.85*

*Statistically significant at $\chi^2 = 3.84$, $P = 0.05$

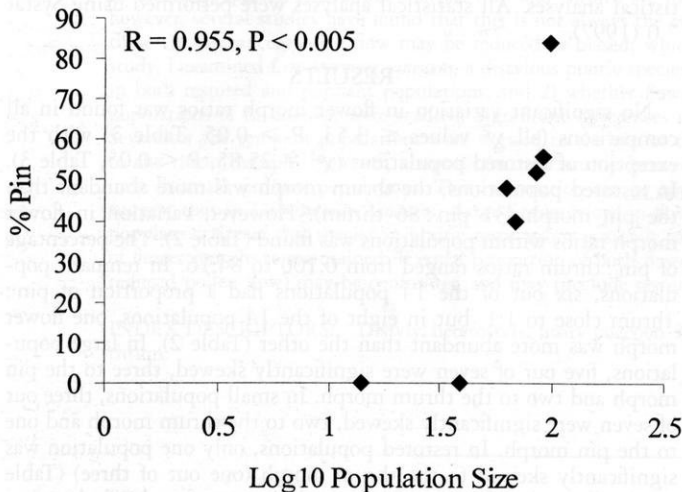


Fig. 1. Relationship between population size and the pin morph in small populations-remnant of *Litbospermum canescens*.

(Baker 1961, Levin 1972, Weller 1980, and references in Barrett 1992a). In this study, I found that many *Litbospermum canescens* populations, both restored and remnant (small and large), had a skewed flower morph ratio, but other populations had equal proportions of the two flower morphs. In addition, in the small remnant populations, I found a statistically significant relationship between population size and the abundance of a flower morph.

Based upon these findings, what is the significant impact of having a skewed pin : thrum ratio for a heterostylous species such as *L. canescens* in remnant and restored prairies? In populations of *L. canescens* found in both remnant and restored prairies, the main impact of a skewed ratio will be at the reproductive level, especially in the movement of pollen (i.e., pollen flow) within a population. Compatible pollen is needed for successful production of seeds in heterostylous species (see references in Barrett 1992a). Many studies have shown that production of pollen and pollen loads on stigmas among these flower morphs are different (see references in Dulberger 1992). Lloyd and Webb (1992) determined that although pin flowers receive more pollen than thrum, more legitimate pollinations occur on thrum flowers. In other words, thrum pollen is more likely to go to a pin stigma than vice versa. This suggests that if one morph is extremely abundant or only one flower morph is present, movement of pollen can be affected, resulting in no seed set or very low reproductive output.

The presence of *Litbospermum canescens* in a prairie remnant suggests a high quality prairie or a virgin prairie condition (Kirt 1995). In a restored prairie, it suggests that the restoration is achieving a plant diversity with spring components similar to those found in a rem-

nant prairie. However, the reintroduction of this species is not an easy task in prairie restorations. For example, only three restorations in this study were found with *L. canescens*. Several reasons have been listed for the failure of such reintroductions: 1) seeds are not collected at the right time (i.e., late spring—early summer) and are not included in the seed mixes (Ray Schulenberg, pers. comm.), 2) seeds fail to germinate and seedlings fail to establish (Eric Ulaszek, pers. comm.) because *L. canescens* seeds have a hard seed coat and may need a pre-germination treatment (e.g., scarification), or the species may be semiparasitic and the seedlings may require a host (Shirly 1994), and 3) the plant is killed by deer browsing (Bob Lootenz, pers. comm.).

In addition to these problems, population size, isolation, plant propagation, and founder effect may create additional problems for *Litbospermum canescens* and other heterostylous species in a restoration. For example, in this study the three restored prairies that were studied had very small population sizes of less than 100 individuals (Table 2), and they were isolated from other *L. canescens* populations. This type of isolation and small population size in other self-incompatible species has resulted in lower reproductive outputs (Byers and Meagher 1992, Byers 1995, Molano-Flores and Hendrix 1999). For a small, isolated population of a heterostylous species with a skewed flower morph, reproductive output can be even lower.

Besides the size and isolation of populations as potential problems for this species, propagation techniques and the quality of the founding population (i.e., gene pool) may be of concern for heterostylous species, in general. For example, *Litbospermum canescens* can be propagated via cuttings (Rock 1974); if care is not taken to recognize the different flower morphs, a restoration may end up with one flower morph and also a limited gene pool. Finally, the quality of the founding population may play an important role in the persistence of the species in a restoration. For example, if the founding population is small, has few genotypes, and is skewed to one flower morph, the persistence of such a population may be in question.

In general, it is recommended that restorations that attempt to establish *Litbospermum canescens* or other heterostylous species, such as *Houstonia caerulea* (blueets), insure that both flower morphs are present. Restorations should aim for large populations with more than 100 individuals and a pin : thrum ratio close to 1:1. However, having a large population does not insure a pin : thrum ratio close to 1:1, as the data on this paper have shown (Table 2), but may prevent the loss of the population as the result of stochastic events. If a large population can not be achieved, but the species is desired in the restoration, then the main emphasis should be placed in achieving a population with a ratio of pin : thrum close to 1:1 individuals. However, trying to achieve this goal is not an easy task especially if it is attempted from seeds. The only way to identify pin and thrum individuals is when the plant is blooming. Nonetheless, collecting seeds from populations with a close 1:1 proportion may increase the chances of collecting both flower morphs. Once the population is

established, additional hand plantings of flowering individuals will be needed to achieve this 1:1 proportion of pin and thrum individuals if the population is skewed.

Additional studies are needed to determine if the results found in this study are the general patterns found in other heterostylous prairie species. It is important that people doing prairie restorations realize that prairie species have different reproductive needs and that the presence of different flower morphs can influence the reproductive success of a species. If we do not include all the elements that are needed for successful reproduction, we may be jeopardizing the persistence of species in our restorations. Although we may be able to include the species in the restoration, in the end they may not persist.

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A Comparison of Management Techniques on Plant Species Composition and Biomass in a Tallgrass Prairie Restoration

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Fire is often employed as a management tool in tallgrass prairie restorations to control non-native species and to re-create ecosystem dynamics associated with historical disturbance regimes. Mowing has been suggested as an alternative management technique, and it may partially simulate grazing activity by native ungulates. We compared the effects of burning and mowing on plant species composition and biomass in a 32-ha, six year old tallgrass prairie restoration in northern Illinois. Burning was conducted in early spring (1996) and mowing in early summer (1996). Standing vegetation was clipped within 10, 0.5-m² quadrats chosen randomly from within each of six 0.6-ha plots with two replicates per each treatment and control. Plots were sampled in June and October of 1996 (before and after mowing) and again in 1997. Species diversity did not differ significantly among treatments, yet total mean biomass did. In June 1996, total biomass was greatest on burned plots, which was largely attributed to growth of native forbs. Native grasses (mainly warm-season perennials) showed an approximate 2.5-fold increase in biomass from June to October of both years on control and burned plots but remained fairly constant on mowed plots over time. *Melilotus alba*, an invasive, non-native forb, responded positively to mowing and burning in the year following manipulations, forming dense colonies that were patchily distributed at the site.

INDEX DESCRIPTORS: aboveground biomass, diversity, fire, Illinois, *Melilotus alba*, mowing, tallgrass prairie.

Prior to European settlement, the tallgrass prairie covered 55–61% of Illinois' land area but now occupies less than 0.01% of the state (Neely and Heister 1987). What remains of the native prairie exists mainly as small, isolated patches. Consequently, there is an interest in its restoration and the reintroduction of the disturbance processes, such as fire and grazing, which shaped the tallgrass prairie communities. These disturbances can influence prairie vegetation (e.g., aboveground biomass and species diversity) and ecosystem dynamics, both of which vary temporally with the frequency of disturbance. For example, fire can increase short-term aboveground net primary productivity on infrequently burned or previously unburned sites as compared to unburned prairies or those subjected to long-term persistent annual burning (Hulbert 1986, Seastedt and Knapp 1993, Briggs et al. 1994, Blair 1997). Annual burning also has the potential to reduce species richness and diversity over time by enhancing dominance of matrix species, like C₄ grasses (Abrams and Hulbert 1987, Collins and Gibson 1990). Furthermore, different fire frequencies affect the availability of nutrients, such as nitrogen and carbon, by altering soil temperature, soil moisture, and belowground biotic processes, namely physiological activity of plant roots and soil microbes (Seastedt and Ramundo 1990, Ojima et al. 1994, Knapp et al. 1998).

Like fire, disturbance introduced by activity of grassland herbivores affects vegetation directly through removal of aboveground biomass and indirectly by altering competition and nutrient cycling. Selective grazing of warm season (C₄) grasses by both native and domestic ungulates (e.g., bison and cattle) can depress abundance of these dominant species and enhance diversity of native forbs (Damhoureyeh and Hartnett 1997, Collins et al. 1998). Resulting soil compaction by trampling and wallowing may facilitate colonization by ruderal species (*sensu* Grime 1979). Nutrient input from herbivore

urine and feces enhances plant productivity within deposition patches and further acts to increase spatial heterogeneity of the habitat (Steinauer and Collins 1996, Williams 1997). Moreover, interaction of grazing and fire disturbances, such as selective grazing of recently burned sites by bison and inhibition of fire propagation through recently grazed areas, was most likely important in shaping spatial and temporal dynamics of historical tallgrass prairie communities (Knapp et al. 1999).

Fire treatments are generally used in the management of restored prairies to approximate historical disturbance regimes and maintain the predominance of native grassland species. In restored prairies of the Midwest, prescribed burning during the dormant season (e.g., early spring or late fall) is commonly implemented to control invasive, woody plant species and non-native species (Adams et al. 1982, McClain 1986). In restoration sites where burning or the reintroduction of large ungulates is not possible, mowing has been suggested as an alternative management technique (Diboll 1984, Morgan 1997, Packard 1997). Like grazing, mowing may delay or suppress seed production in flowering plants (Sollenberger 1994) and may enhance diversity, due to competitive release, depending upon timing and frequency (Howe 1999).

Particular attention has focused on the use of prescribed burning and mowing to control aggressive and persistent weed species such as white sweet clover (*Melilotus alba*) in tallgrass prairies (Kline 1984). White sweet clover is a biennial legume, native to Eurasia. It was introduced to North America over 300 years ago for use as a livestock forage crop and soil conditioner (Klemow and Raynal 1981). It tolerates a broad range of environmental conditions and proliferates in habitats associated with tallgrass and mixed-grass prairies. Sweet clover is common in many tallgrass prairie restorations owing to its continued, widespread use in agriculture and the long-

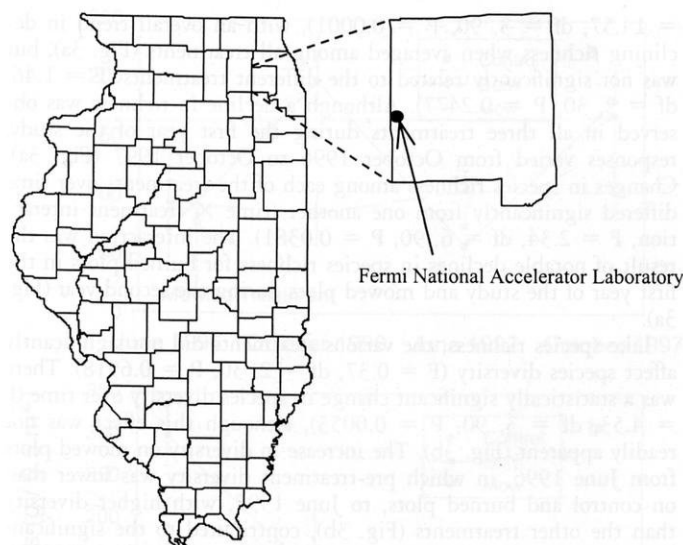


Fig. 1. Location of Fermi National Accelerator Laboratory (Fermilab) in northeastern Illinois. A 32-ha prairie restoration at Fermilab was used as the study site.

term viability of its seeds (Turkington et al. 1978). White sweet clover has been observed to respond positively to dormant season burning, which helps stimulate seed germination (Kline 1984).

We investigated the effects of fire and mowing on plant species composition and plant productivity in a previously unmanaged tall-grass prairie restoration of northern Illinois. In particular, we assessed the effects of spring burning or mowing during the growing season on species richness, species diversity, total aboveground biomass, and aboveground biomass of prairie grasses and forbs. We predicted a positive response of dominant warm-season grasses to spring burning, a corresponding decrease in forbs, and lower species richness and diversity. On the contrary, positive responses of forbs, generally non-dominant species, should be reflected in increased richness or diversity. We also compared the effects of these management techniques on the abundance of white sweet clover. We predicted that productivity, quantified by aboveground biomass, of sweet clover would be enhanced by burning but depressed by mowing prior to flowering.

METHODS

The study site was located in a 32-ha restored prairie at Fermi National Accelerator Laboratory in Batavia, Illinois (Fig. 1). Prior to 1990, this site was an agricultural field planted with either corn or soybeans. The area was broadcast seeded with a mixture of native grasses and forbs in the spring of 1990. Consequently, vegetational composition of this grassland was relatively homogeneous. No management regimes (i.e., burning, mowing, or grazing) were implemented following seeding. The plant community was dominated by warm-season perennial grasses, primarily big bluestem (*Andropogon gerardii*) and Indian grass (*Sorghastrum nutans*), typical of mesic tall-grass prairie. A variety of forb species were also present, including native and non-native species, with tall goldenrod (*Solidago altissima*) and Queen Anne's lace (*Daucus carota*) common throughout the site (Table 1). In 1996, habitat manipulations were carried out on six, 0.8-ha experimental plots, with two replicates per each of three treatments (fire, mowing, and control). Concurrent with common management regimes in northern Illinois, burning was conducted in mid-March 1996, during the dormant season, and mowing done in late June 1996. Vegetation was mowed to a height of 20 cm, and

Table 1. Ten most abundant plant species at the study site based upon cumulative biomass throughout the duration of the study.

Scientific Name	Common Name
<i>Andropogon gerardii</i>	Big bluestem
<i>Coreopsis tripteris</i>	Tall coreopsis
<i>Daucus carota</i> ^a	Queen Anne's lace
<i>Helianthus grosseserratus</i>	Sawtooth sunflower
<i>Melilotus alba</i> ^a	White sweet clover
<i>Panicum virgatum</i>	Switchgrass
<i>Silphium integrifolium</i>	Rosinweed
<i>Solidago altissima</i>	Tall goldenrod
<i>Solidago rigida</i>	Stiff goldenrod
<i>Sorghastrum nutans</i>	Indian grass

^aDenotes non-native species

resulting litter was not removed. Standing aboveground biomass was sampled using ten, 0.5-m² quadrats per plot in June (prior to mowing) and October of 1996 (at the end of the growing season) and again in June and October of 1997. Sampled vegetation represented the current year's growth (green vegetative tissue in June and standing dead plus green tissue in October); plant litter was not collected. After the vegetation of each quadrat was collected, it was separated by species, oven-dried at 100°C to a constant weight, and biomass recorded. We then calculated the total biomass of vegetation from each quadrat in each plot for every sampling period.

Likewise, species diversity of each quadrat within a plot was computed using Simpson's diversity index ($1 - \sum p_i^2$); indices of the 10 quadrats within a plot were then averaged. Simpson's index is most sensitive to abundant species (Krebs 1989). Because of the absence of many rare species at our study site, we felt this index would be more conservative in detecting community changes attributed to the different treatments.

Changes in biomass, species richness, and species diversity per treatment over time were analyzed using separate, one-way repeated measures Analysis of Variance (rmANOVA) with quadrats nested within treatments to avoid pseudoreplication (Hurlbert 1984). Significance was determined at $\alpha = 0.05$.

RESULTS

There were significant changes in mean total biomass among the different treatments ($F = 10.84$, $df = 2, 30$, $P = 0.0003$). In June 1996, several months after the fire, mean biomass was 18% lower on control plots and 37% lower on mowed plots as compared to burned plots (Fig. 2). Total biomass on control and burn plots was greater in 1996 than in 1997, which resulted in a significant time effect ($F = 11.74$, $df = 3, 90$, $P = 0.0001$). Biomass remained relatively constant on the mowed plots except for the direct effects of mowing, in which total biomass on these plots was reduced by 40% in October 1996 as compared to pre-treatment levels (Fig. 2). Changes in total biomass among each of the treatments also differed significantly from one another over time (time \times treatment interaction, $F = 7.80$, $df = 6, 90$, $P = 0.0001$). The significant interaction was due to the decline in total biomass on control and burned plots from October 1996 to June 1997, as opposed to the increase in biomass on mowed plots during this period, with a return to pre-treatment levels. By June 1997, biomass among treatments had roughly converged. In October 1997, biomass measurements on control and mowed plots were similar to their June 1996 values, but

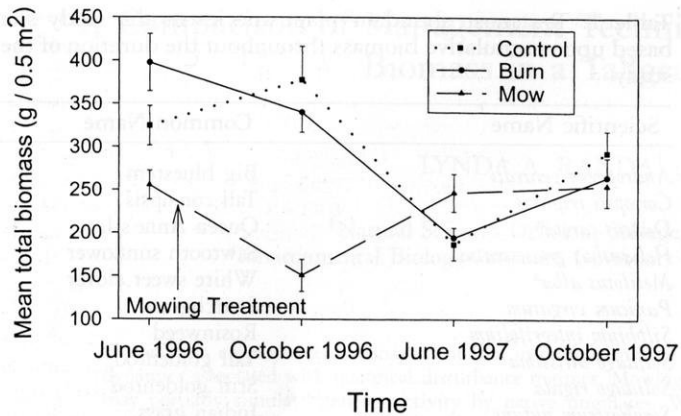


Fig. 2. Change in mean (\pm SE) standing aboveground biomass of vegetation over time for fire, mowing and control treatments.

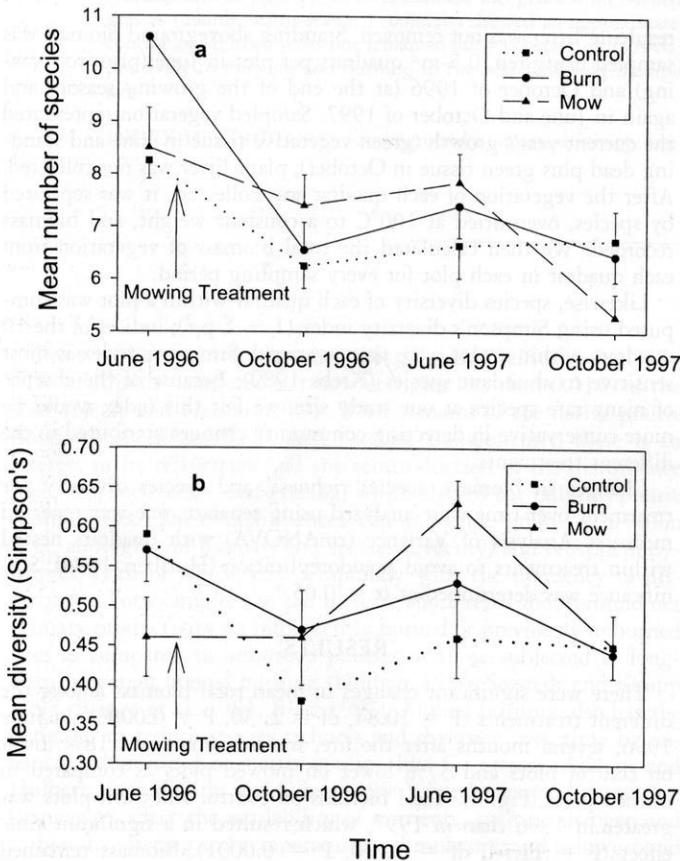


Fig. 3. Change in mean (\pm SE) (a) plant species richness and (b) plant species diversity over time for fire, mowing and control treatments. Species richness and diversity represent averages between replicates of each treatment. Species diversity was computed using Simpson's diversity index.

biomass on burned plots was substantially lower from initial (June 1996) values (Fig. 2).

Forty different species were identified from the samples we collected, but not all occurred in each treatment plot at each time period (Fig. 3a). Species richness changed significantly over time (F

$= 14.57$, $df = 3, 90$, $P = 0.0001$), with an overall trend in declining richness when averaged among all treatments (Fig. 3a), but was not significantly related to the different treatments ($F = 1.46$, $df = 2, 30$, $P = 0.2477$). Although a decline in richness was observed in all three treatments during the first year of the study, responses varied from October 1996 to October 1997 (Fig. 3a). Changes in species richness among each of the treatments over time differed significantly from one another (time \times treatment interaction, $F = 2.34$, $df = 6, 90$, $P = 0.0381$). The interaction was the result of notable declines in species richness for burned plots in the first year of the study and mowed plots during the second year (Fig. 3a).

Like species richness, the various treatments did not significantly affect species diversity ($F = 0.37$, $df = 2, 30$, $P = 0.6918$). There was a statistically significant change in species diversity over time ($F = 4.53$, $df = 3, 90$, $P = 0.0053$), although this effect was not readily apparent (Fig. 3b). The increase in diversity on mowed plots from June 1996, in which pre-treatment diversity was lower than on control and burned plots, to June 1997, with higher diversity than the other treatments (Fig. 3b), contributed to the significant time \times treatment interaction ($F = 2.20$, $df = 6, 90$, $P = 0.0498$). Diversity levels then converged by fall 1997.

We also evaluated species composition by identifying three broad functional groups: native grasses, native forbs, and non-native forbs. Native grass biomass differed significantly among treatments ($F = 5.25$, $df = 2, 30$, $P = 0.0111$) due predominantly to effects of mowing (Fig. 4a). The change in grass biomass over time was also statistically significant ($F = 8.94$, $df = 3, 90$, $P = 0.0001$). Biomass of grasses on burned and control plots showed the same general patterns, peaking in October of both years (Fig. 4a). This seasonal change was attributed to increased biomass of the dominant warm-season grasses, which accounted for approximately 57% of the total aboveground biomass at these times. Due to treatment responses, grass biomass on mowed plots remained relatively constant over time, with an approximate 50% reduction in biomass in October 1996 and 1997 as compared to the other treatments (Fig. 4a). The lower biomass on mowed plots in October 1996 was a direct effect of mowing or non-selective removal of aboveground biomass, whereas grass biomass on mowed plots in October 1997 reflected protracted effects of mowing through reduced dominance of warm-season grasses. Initial biomass differences among the control and burned plots plus the effects of the mowing treatment (Fig. 4a) contributed to the significant interaction of treatment differences over time ($F = 3.19$, $df = 6, 90$, $P = 0.0070$).

Like the grasses, native forb biomass differed significantly among treatments ($F = 5.38$, $df = 2, 30$, $P = 0.0101$); these differences were most apparent in the first year of the study (Fig. 4b). A significant time effect ($F = 23.14$, $df = 3, 90$, $P = 0.0001$) resulted from an overall decline in native forb biomass on burned and control plots over the study period (Fig. 4b). Native forb biomass changes over time differed significantly among each of the three treatments (time \times treatment interaction, $F = 5.67$, $df = 6, 90$, $P = 0.0001$); however, these patterns differed from those observed for the grasses (Fig. 4a, b). Highest native forb biomass occurred in June 1996 on the burned plots several months after the fire, with average native forb biomass 33% and 50% greater than forb biomass on control and pre-treatment mowed plots, respectively. This effect was short-lived, as a 44% reduction in biomass was recorded on the burned plots by the next sampling period (October 1996). Biomass among the different treatments converged by June 1997 (Fig. 4b).

White sweet clover (*Melilotus alba*) was one of the most common non-native forbs at the site and comprised 25–68% (mean \pm SE = 0.47 ± 0.10) of non-native forb biomass, making it the single most abundant, non-native forb at the study site. Hence, response of white

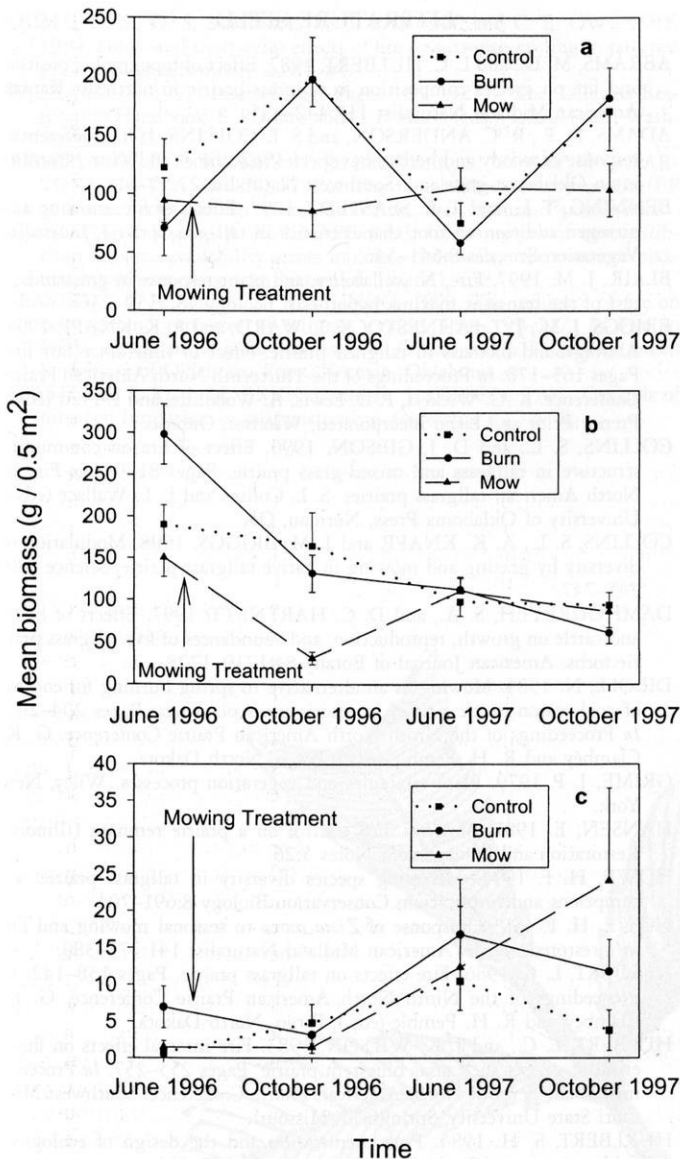


Fig. 4. Change in mean (\pm SE) biomass of (a) native grasses, (b) native forbs, and (c) white sweet clover over time for fire, mowing and control treatments.

sweet clover abundance, rather than all non-native forbs, to the treatments is presented here. White sweet clover biomass changed significantly over time ($F = 3.18$, $df = 3, 90$, $P = 0.0277$), responding positively to both fire and mowing treatments with an approximate one-year time lag (Fig. 4c). However, variance in sweet clover abundance in 1997 precluded detection of significant treatment effects ($F = 0.89$, $df = 2, 30$, $P = 0.4214$). The time \times treatment interaction was also not significant ($F = 1.02$, $df = 6, 90$, $P = 0.4157$). The large variances associated with sweet clover biomass were indicative of the patchy distribution of this species at the study site. One of the mowed plots, in particular, was completely dominated by white sweet clover during the second year of the study.

DISCUSSION

Fire and mowing had different impacts on overall plant productivity, assessed by total aboveground biomass measurements. Total

biomass was most altered by mowing, with a significant reduction in biomass measured at the end of the first growing season but a return to pre-treatment levels by the following year. This recovery in biomass can be partly attributed to the dominant native grasses, particularly big bluestem, which exhibited greater biomass on the mowed plots compared to other treatments in the second summer (June 1997) of our study. Aboveground plant growth appeared to be stimulated the greatest by the spring fire. The peak in biomass observed on the burned plots several months after the fire was mainly attributed to native forbs, which accounted for approximately three-fourths of the total standing aboveground biomass at that time. Comparison with the control and pre-treatment mowed plots suggests this can be attributed to fire effects, although lack of pre-treatment data may confound whether other factors contributed to the positive response observed on the burned plots. Relatively high productivity in the growing season following fire has been previously documented (Hulbert and Wilson 1983, Seastedt et al. 1991, Briggs et al. 1994). This is due, in part, to the release of accumulated, previously unavailable nitrogen in the litter and soil of unburned or infrequently burned tallgrass prairie (Blair 1997, Turner et al. 1997) that then can be utilized for plant growth in the growing season that follows a spring fire. However, high nitrogen volatilization during fire represents a significant source of nitrogen loss (Seastedt and Ramundo 1990) resulting in nitrogen-limited systems in frequently burned prairies (Ojima et al. 1994). Short-term increases in productivity of prairie following fire are also related to greater light availability (Blair 1997). Solar radiation warms exposed soils following a spring fire, which in turn may facilitate increased activity of microbes associated with nitrogen cycling. Litter accumulation and lessened opportunity for soil warming may help explain why mowing did not eventually generate an equivalent peak in total biomass.

Species richness and diversity varied over time but were not significantly related to our treatments. The lack of significant treatment effects reflects overall trends over the entire study period but does not preclude notable changes that may be biologically meaningful, like the observed peak in species richness on burned plots several months after the fire. The burned plots also exhibited a trend of generally lower richness and diversity by the end of the growing season (October) as compared to earlier in the growing season (June). This reflected dominance of warm-season grasses at the end of the growing season, which comprised over half of the total aboveground plant biomass in October of both years of the study. Similar peaks in grass biomass on the control plots were not reflected in any apparent trends in species richness or diversity. Additionally, grass biomass on mowed plots did not exhibit the same seasonal fluctuations as the control and burned plots, due to overall reduction in biomass in October 1996 and decreased abundance of warm-season native grasses in October 1997 from competition with the non-native forb, white sweet clover.

For tallgrass prairie in general, the number of forb species in a community tends to exceed that of the grasses (Risser et al. 1981). Thus, we predicted that a positive response of forbs to disturbance would result in greater richness or diversity. This was observed for species richness several months after burning, due largely to a positive response of native forbs to fire, but response of forbs to disturbance did not result in a significant treatment effect on species richness over the entire course of the study. However, native forb biomass did respond significantly to the burning treatment.

At our site, one-time mowing depressed warm-season grass dominance by the end of the growing season in the year of manipulation. This effect may be similar to native prairies subjected to a single grazing event by bison but through different mechanisms; bison will selectively feed upon warm-season grasses (Damhoureyeh and Hartnett 1997), whereas mowing is a non-selective process. Because such

grazing involves removal of aboveground graminoid vegetation, native forb growth can be facilitated through competitive release. However, reduction of C₄ grass biomass on our mowed plots was not compensated by increased native forb abundance but rather an increase in non-native forbs, such as white sweet clover (*M. alba*) and field thistle (*Cirsium arvense*).

White sweet clover present at the study site formed dense colonies that were capable of out-competing native prairie species in disturbed locations, such as experimentally burned or mowed patches. Dense stands of sweet clover were also observed along linear areas of disturbance, such as walking and vehicle paths. Greatest abundance of sweet clover occurred in the year following experimental mowing, coinciding with increased production of aboveground biomass during the second year of the biennial life cycle. The positive response of white sweet clover to the fire treatment may be related to the competitive advantage of legumes in soils containing less available nitrogen the year following a fire (Towne and Knapp 1996). Widely used management regimes that employ either spring burning or mid-growing season mowing may actually promote sweet clover abundance. Effective methods of its control must target reduction of vegetative growth during the growing season and inhibition of seed production. Because of its biennial life cycle, this requires appropriately timed burning or mowing over at least two successive years (e.g., early spring burn in 1st year followed by late spring burn in 2nd year; Kline 1984, Hansen 1987).

It is important to note that the natural disturbances of fire and grazing commonly co-occurred in historical tallgrass prairie (Howe 1994). Combinations of fire and grazing or fire and mowing result in different ecosystem responses than if either one of these treatments were implemented alone (Benning and Seastedt 1997, Collins et al. 1998, Knapp et al. 1999). Heterogeneous distribution of wildfires, grazing patterns, and disturbance interactions contribute to spatial heterogeneity of grassland systems. Such effects are not easily duplicated by human-induced disturbances, such as burning and mowing, which tend to be more uniformly distributed across a local area. Furthermore, more rapid recycling of nutrients (e.g., nitrogen) following grazing as compared to mowing could variously affect spatial and temporal heterogeneity of native grasslands. Irregular occurrence of non-anthropogenic fires and non-foraging disturbances associated with activity of large grazers, such as vegetation trampling, also contribute to temporal heterogeneity of prairie plant communities. Seasonal changes in the microhabitat of bison wallows (standing water in spring and dry, compact soil in summer) can influence temporal dynamics of plant species composition by alternatively supporting species adapted to wet or dry environments (Knapp et al. 1999). Hence, rotation of burning and mowing amongst experimentally manipulated patches within tallgrass prairie restorations, varied over time, is needed to assess the ability of land managers to duplicate community heterogeneity promoted by historical disturbances of tallgrass prairie.

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A Sixteen Year Assessment of Vegetational Changes in Prairie Seed Broadcast and Seedling Transplant Sites

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A 0.63 ha clay and rubble area at College of DuPage in Glen Ellyn, IL was planted in 1984 with 28 prairie species by using two restoration methods, seed broadcast and seedling transplant. The Wilhelm Assessment Method was used to compare vegetational changes for these two methods over a 16 year period. Weeds were not removed during the study. Burning was done annually beginning in 1988. To record vegetational changes, plant species were identified and tallied along 21 north-south transect lines. The transects were 0.5 m wide and spaced 10 m apart; they varied in length from 3.8 to 55.2 m. A seed broadcast area of 196.7 m² and a seedling transplant area of 42.7 m² were evaluated from 1984-1987, 1991-1992, and 1998-1999. There was a slow and steady decline in the number of weed species and an increase in the prairie species for both methods of reconstruction. Forty-nine weed species disappeared in the seed broadcast area while eight additional prairie species, not in the original planting, became established. Fifty-one weed species disappeared in the seedling transplant area while 10 additional prairie species, not in the original planting, became established. Populations of *Melilotus alba* and *M. officinalis* are increasing and may pose a threat unless controlled. After 16 growing seasons, the index value for the seedling transplant area increased from 20.10 to 30.20, and the seed broadcast area increased from 20.74 to 30.11; there was no significant difference ($P > 0.05$) between planting methods. Assuming no immigration from adjacent plantings or residual germination from a seed bank, the highest theoretical index values the plantings could have achieved were 29.71 for the seedling transplant area and 29.79 for the seed broadcast area. Succession toward a prairie plant community can be achieved by either seed broadcast or seedling transplant methods.

Annual springtime fires for the past fourteen years did not increase the population size of either big bluestem or Indian grass. Meadow voles foraged most heavily on the underground portions of purple coneflower, prairie blazing star, and wild quinine.

INDEX DESCRIPTORS: vegetational changes, quantitative analyses, Wilhelm Assessment Method, coefficient of conservatism, index value, weed.

The reestablishment of prairie species by seeding or transplanting on areas after the original vegetation was completely removed has been accomplished in several areas of the United States (Dale and Smith 1983). Many researchers, restorationists, and reconstructionists have reported on the success of prairie plantings, beginning with the historic first planting of prairie at the University of Wisconsin Arboretum. Many assessment analyses of prairie restoration or reconstruction sites have been qualitative (i.e., good or poor) and not in terms of consistent standards (Harper 1983, Sperry 1983).

Quantitative analyses of prairie restoration projects include Anderson and Cottam's (1970) "prairie continuum" used to describe the frequency of vegetational change in the H. C. Greene Prairie in the University of Wisconsin Arboretum. Also, Woehler and Martin (1983) documented annual vegetation changes from 1975 to 1980 in Wisconsin using stratified random measurements to calculate the "importance values" of plants. Dale and Smith (1983) compared the percent cover of prairie grasses and weeds for five years to report the successional changes in a reconstructed prairie in Arkansas. Finally, Liegel and Lyon (1986) noted vegetational trends through five years for a prairie restoration site in southern Wisconsin using percent cover for each species present.

This study quantitatively compared the vegetational changes of a seed broadcast area with a seedling transplant area over a 16 year period with no weed removal. Annual spring fire began after the first four years. The effects of fire and meadow vole herbivory are also discussed for selected species.

SITE LOCATION AND DESCRIPTION OF STUDY AREA

The study site is in a section of the area now known as the Russell R. Kirt Prairie on the campus of College of DuPage in Glen Ellyn, Illinois, NW ¼ of Section 27, Township 39, Range 10 in DuPage County, Illinois. The study area of 0.63 ha is roughly rectangular in shape (Fig. 1). Approximately one-half of the site, on the south side, is bordered by thick stands of cattails (*Typha latifolia* L. and *T. angustifolia* L.) and sandbar willow (*Salix interior* Rowlee), and lawn grass borders the north side.

Prior to 1965, the study area was farmed. From 1965 to 1975, the area remained fallow. Twenty to 25 cm of gravel was spread on the area during 1975, and it served as a parking lot until 1984. During spring 1984, clay and rubble subsoil from construction on the College of DuPage campus was dumped on the study site and contoured from an elevation of 228.1 m to 230.1 m above sea level. The restoration area was then top-dressed with 7-10 cm of black soil from another construction site on campus. Soil characteristics of the site were analyzed in 1987 (Table 1).

METHODS

During early April, 1984, seeds from 15 prairie species (Table 2) were planted into a 50-50 mixture of "Jiffy Mix" (Ball Seed Company) and sterilized black soil in the College of DuPage greenhouse. During early to mid-May 1984, the seedlings were transplanted to individual jiffy pots and, after a week, acclimatized outside in a semi-shaded area. During late May and early June 1984, the acclimatized

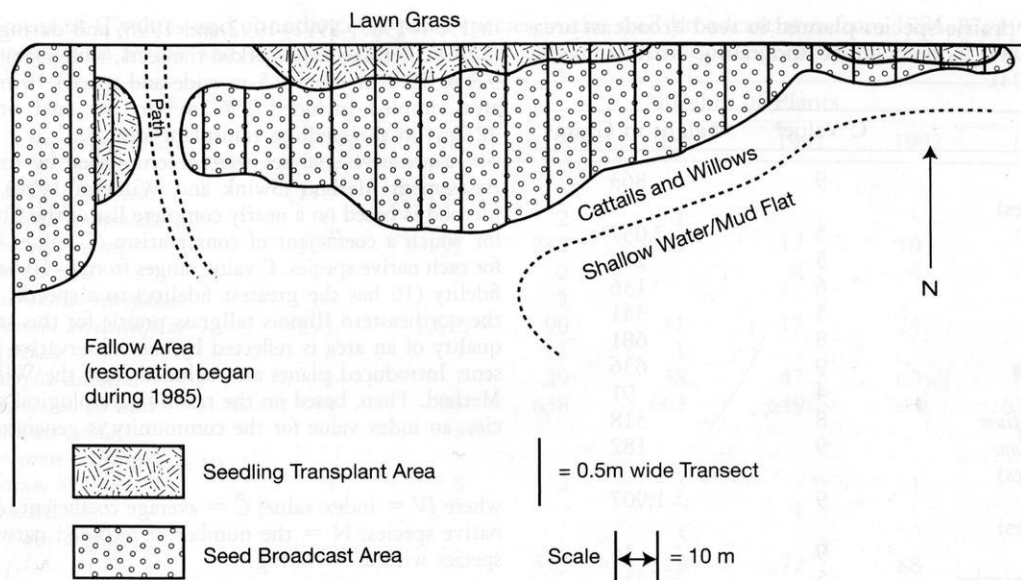


Fig. 1. Russell R. Kirt Prairie.

Table 1. Site soil characteristics.^a

Elements	PPM (Nitric/Chloric Acid Digest Test)
P	600
K	6,000
Ca	37,600
Mg	23,000
S	2,600
Zn	80
B	58
Mn	783
Fe	28,627
Ca	15
Al	23,185
Na	<69

^aThere was 3.57% organic matter in the soil; its pH was 8. The soil data is a composite of three random samples. It was analyzed by Department of Soil Science, University of Wisconsin Extension, Madison, WI 53705-4354

seedlings were transplanted to the reconstruction site (Fig. 1). The entire reconstruction site was disked to a depth of 5–8 cm to level the soil and break up soil clumps prior to transplanting and seed broadcasting.

A seed mixture of 24 prairie species (Table 3) was broadcast adjacent to the seedling transplant area (Fig. 1) from mid-May to early June 1984. Wild bergamot (*Monarda fistulosa* L), switchgrass (*Panicum virgatum* L), and foxglove beard tongue (*Penstemon digitalis* Nutt.) were present but not knowingly included in the seed broadcast mixture. Seed was cleaned as well as possible by hand using screens; structures attached to seeds, such as pappus and calyces, were not removed. Seeds were broadcast, lightly raked into the soil, and then compacted into the soil with a 90 kg lawn roller.

All seeds were hand-collected during 1983 from sites within a 40

Table 2. Seedlings of prairie species planted in seedling transplant area during spring, 1984. Nomenclature and rating is from Swink and Wilhelm (1994).

Species	C Value ^a	Number of Seedlings
<i>Amorpha canescens</i>	9	144
<i>Baptisia leucantha</i>	8	72
<i>B. leucophaea</i>	10	144
<i>Coreopsis palmata</i>	6	357
<i>Echinacea pallida</i>	8	251
<i>Eryngium yuccifolium</i>	9	196
<i>Liatris pycnostachya</i>	8	306
<i>Parthenium integrifolium</i>	8	288
<i>Penstemon digitalis</i>	4	23
<i>Petalostemum candidum</i>	9	681
<i>P. purpureum</i>	9	144
<i>Potentilla arguta</i>	9	36
<i>Solidago rigida</i>	4	216
<i>Sporobolus heterolepis</i>	10	5,256
<i>Verbena stricta</i>	4	72
Total	115	

^aAverage C (Coefficient of Conservatism) Value = 7.67

IV (Index Value) = 29.71 (for prairie species planted in seedling transplant area)

km radius of the reconstruction site at College of DuPage to ensure local genotypes. Seeds were cleaned as well as possible by hand using screens. They were then kept in cold storage until early February, 1984. The seeds were then stratified in fine damp sand and refrigerated at 4°C until planting. Legume seeds were scarified and inoculated with their appropriate *Rhizobium* (Source: Liphatech, Inc., 3101 West Custer Avenue, Milwaukee, WI 53209).

Oat and wheat straw were lightly scattered over both the seed broadcast and seedling transplant areas to conserve soil moisture and

Table 3. Seeds of prairie species planted in seed broadcast area during spring, 1984. Nomenclature and rating is from Swink and Wilhelm (1994).

Species	C Value ^a	Weight in Grams
<i>Amorpha canescens</i> (including calyces)	9	863
<i>Andropogon gerardii</i>	5	7,037
<i>A. scoparius</i>	5	272
<i>Coreopsis palmata</i>	6	136
<i>C. tripteris</i>	5	341
<i>Echinacea pallida</i>	8	681
<i>Eryngium yuccifolium</i>	9	636
<i>Lespedeza capitata</i>	4	91
<i>Parthenium integrifolium</i>	8	318
<i>Petalostemum candidum</i> (including calyces)	9	182
<i>P. purpureum</i> (including calyces)	9	1,907
<i>Potentilla arguta</i>	9	36
<i>Pycnanthemum virginianum</i> (including chaff)	5	454
<i>Ratibida pinnata</i>	4	726
<i>Rudbeckia hirta</i>	1	204
<i>Silphium laciniatum</i> (including bracts)	5	1,907
<i>S. perfoliatum</i> (including bracts)	5	82
<i>S. terebinthaceum</i> (including bracts)	5	341
<i>Solidago rigida</i> (including pappus)	4	772
<i>Sorghastrum nutans</i>	5	200
<i>Spartina pectinata</i>	4	590
<i>Sporobolus heterolepis</i>	10	341
<i>Vernonia fasciculata</i> (including pappus)	5	114
<i>Veronicastrum virginicum</i> (including chaff)	7	145
Total	146	

^aAverage C (Coefficient of Conservatism) Value = 6.08

IV (Index Value) = 29.79 (for prairie species planted in seed broadcast area)

protect the seedlings from direct sunlight. Both areas were irrigated until 1 July 1984 whenever rainfall was insufficient.

For both planting methods, mesic-xeric species, such as lead plant (*Amorpha canescens* Pursh), were broadcast on the higher elevations and mesic-hydric species, such as prairie dock (*Silphium terebinthaceum* Jacq.), on the lower elevations. Whenever possible, species associations as described by Swink and Wilhelm (1994) were planted together.

The choice of plantings was based on seed availability, seed germination and competitiveness (Schulenberg 1972, Schramm 1978), time and space available to grow and transplant seedlings, and overall aesthetics. Although a somewhat different array of species was planted in each area, there was no significant difference ($P > 0.05$) in their average numerical rating ($\chi^2 = 0.273$; Goodness of Fit, Zar 1984). Annual springtime fires began in 1988.

To record vegetational changes, plant species were identified and tallied annually along 21 north-south transect lines during October,

in 1984–1987, 1991–1992 and 1998; and during August in 1999 (Fig. 1). Permanently marked transects, which ranged in length from 3.8 to 55.2 m, were 0.5 m wide and spaced 10 m apart. The total area sampled included 196.7m² in the seed broadcast area and 42.7m² in the seedling transplant area.

Quantitative analyses were accomplished by using the Wilhelm Assessment Method (Swink and Wilhelm 1994). This assessment method is based on a nearly complete list of the Chicago region flora for which a coefficient of conservatism (C value) has been assigned for each native species. C value ranges from 0–10 based on the species fidelity (10 has the greatest fidelity) to a specific habitat, which is the northeastern Illinois tallgrass prairie for this study. The floristic quality of an area is reflected by the conservative plant species present. Introduced plants are excluded from the Wilhelm Assessment Method. Then, based on the taxon's autecological values for the species, an index value for the community is generated as follows:

$$IV = \bar{C}\sqrt{N}$$

where IV = index value; \bar{C} = average coefficient of conservatism for native species; N = the number of recorded native taxa, including species with a "0" rating.

RESULTS AND DISCUSSION

According to Swink and Wilhelm (1994), 89% of our native plants have been given a value of 4 or higher and accommodate a wide array of specialized plant communities. Plant species with a C value of less than 4 are considered "disturbance species or weeds;" that is, they are plants that thrive in disturbed and degraded areas and are not part of a stable ecosystem. These can be native or introduced plants. For this study, plant species with a C value of 4 or above belong to the prairie community (Voigt and Mohlenbrock 1978, Kirt 1995).

Seed Broadcast Area

Table 4 lists the plant species found growing in the seed broadcast sample area from 1984 to 1999. There were 28 prairie species present with a numerical rating of 4 or above in 1999 (Table 4); of these 28 species, 22 were planted in 1984 (Table 3). The Index Value (IV) from 1984 to 1999 increased from 20.74 to 30.11 (Fig. 2). The maximum IV that the seed broadcast area could achieve is 29.79 (Table 3) without immigration from adjacent plantings or germination from a seed bank.

The IV increase and the decrease of weed species indicates that the seed broadcast reconstruction area has been progressing toward prairie; but, without additional species immigration or residual germination from a seed bank, the maximum rating IV will remain at approximately 30 (Table 3). In his "successional restoration" studies, Betz et al. (1995) suggested that after initial planting of prairie species that have a wide range of tolerances (Stage 1), additional species can be added to enrich the prairie. This study suggested additional species establishment in the prairie proper was unlikely probably due to the extensive root system of the prairie matrix. However, some species may establish themselves into the seed broadcast along the periphery of the site or in disturbed sites. After 16 growing seasons, side-oats grama (*Bouteloua curtipendula* (Michx.) Torr.), dogbane (*Apocynum sibiricum* Jacq.), showy tick trefoil [*Desmodium canadense* (L.) DC.], prairie blazing star (*Liatris pycnostachya* Michx.), rosinweed (*Silphium integrifolium* Michx.), wild bergamot, switchgrass, and foxglove beard tongue were species found growing along the perimeter of the seed broadcast area that were not knowingly in the original species planting.

Forty-nine weed species, that is, native species with C < 4 and introduced species, disappeared from the seed broadcast area (Table

Table 4. Assignment of C values and abundance of plant species in the seed broadcast area from 1984–87, 1991–92, and 1998–99. Nomenclature is from Swink and Wilhelm (1994). Asterisk indicates introduced species.

C Value	Recorded Taxa	Number of Plants							
		1984	1985	1986	1987	1991	1992	1998	1999
*	<i>Abutilon theophrasti</i>	110	109	3					
0	<i>Acalypha rhomboidea</i>	6	3	2	1				1
*	<i>Agropyron repens</i>	123	191	232	169	12	10	2	
*	<i>Agrostis alba</i>	13	5	2		4	4		1
*	<i>Amaranthus retroflexus</i>	16		5					
0	<i>Ambrosia artemisiifolia</i>	193	1,615	90	31	17	24		4
0	<i>A. trifida</i>	1	4	3	1				
9	<i>Amorpha canescens</i>	4	7	29	38	47	69	68	73
5	<i>Andropogon gerardii</i>	540	791	638	662	649	703	676	658
*	<i>Anthemis cotula</i>		1						
2	<i>Apocynum sibiricum</i>								2
*	<i>Arctium minus</i>	5	5	2	3		1		
5	<i>Aster ericoides</i>					1			
4	<i>A. novae-angliae</i>				3				
0	<i>A. pilosus</i>	9	98	379	329	72	88	4	
*	<i>Atriplex patula</i>	16	4						
*	<i>Avena sativa</i>	298							
*	<i>Barbarea vulgaris</i>	56	1						
1	<i>Bidens sp.</i>	4	1						
8	<i>Bouteloua curtipendula</i>					2	3	1	1
0	<i>Brassica kaber</i>	37							
*	<i>Bromus inermis</i>		29	21					
*	<i>Cerastium vulgatum</i>	12		8					
*	<i>Chenopodium album</i>	284	107	1	1				
*	<i>Cichorium intybus</i>	18	72	5	4				
*	<i>Cirsium arvense</i>	63	166	191	158		1		
*	<i>C. vulgare</i>	17	23	23	10				
6	<i>Coreopsis palmata</i>	44	42	43	30	66	89	76	78
5	<i>C. tripteris</i>	281	313	218	172	164	184	77	76
1	<i>Cyperus strigosus</i>	302	76						
*	<i>Dactylis glomerata</i>	2		7	9				
*	<i>Daucus carota</i>	32	33	632	222	58	48		8
4	<i>Desmodium canadense</i>								4
*	<i>Digitaria sanguinalis</i>	127	16						
8	<i>Echinacea pallida</i>	98	103	86	61	44	42	18	21
0	<i>Echinochloa crusgalli</i>	252	6	3					
0	<i>Erigeron annuus</i>						11		
0	<i>E. canadensis</i>		43	9	1				
9	<i>Eryngium yuccifolium</i>	8	7	9	15	15	12	7	5
0	<i>Eupatorium altissimum</i>							2	1
0	<i>Euphorbia supina</i>	33		8					
*	<i>Festuca elatior</i>	20	24	4	5	1			
2	<i>Helianthus grosseserratus</i>		3	2					
*	<i>Hibiscus trionum</i>	76	119	17					
*	<i>Hordeum jubatum</i>	4	18	34	13				
*	<i>Lactuca scariola</i>		10						
0	<i>Lepidium virginicum</i>	1	95	16					
4	<i>Lespedeza capitata</i>			1	1	1	1	1	4
8	<i>Liatris pycnostachya</i>								1
*	<i>Lychnis alba</i>		17						
*	<i>Malva neglecta</i>					1			
*	<i>Melilotus spp.</i>	7			2	5	4	3	22
*	<i>Medicago lupulina</i>					8	3		4
4	<i>Monarda fistulosa</i>		1	3				5	11
*	<i>Nepeta cataria</i>	4	2			1	1	2	1
0	<i>Oenothera biennis</i>		1	1					
0	<i>Oxalis stricta</i>	21	44			3	5		2
1	<i>Panicum capillare</i>	40	5	2					

Table 4. Continued.

C Value	Recorded Taxa	Number of Plants							
		1984	1985	1986	1987	1991	1992	1998	1999
5	<i>P. virgatum</i>		4	8	3	6	6	7	8
8	<i>Parthenium integrifolium</i>	18	4	8	5		2	1	
*	<i>Pastinaca sativa</i>	18							
4	<i>Penstemon digitalis</i>				1	1			1
9	<i>Petalostemum candidum</i>	62	57	45	67	51	43	13	15
9	<i>P. purpureum</i>	102	78	131	110	98	110	104	107
*	<i>Pbleum pratense</i>		4	6			8		
0	<i>Physalis subglabrata</i>								1
*	<i>Plantago major</i>	132	223	55	51	3	3		
0	<i>P. rugelii</i>	19	5	6					
*	<i>Poa annua</i>	13	2						
*	<i>P. pratensis</i>	108	267	204	180	79	62	31	26
0	<i>Polygonum pensylvanicum</i>	203	33					1	1
2	<i>Populus deltoides</i>	24	6	3	4	1	1	1	1
9	<i>Potentilla arguta</i>	1	8	6	4	5	4	3	5
0	<i>P. norvegica</i>	13	28	4					
5	<i>Pycnanthemum virginianum</i>	6	5	2	2		1	2	2
4	<i>Ratibida pinnata</i>	496	573	314	254	253	238	67	81
1	<i>Rhus typhina</i>							1	2
4	<i>Rorippa palustris fernaldiana</i>	16						1	
1	<i>Rudbeckia hirta</i>	134	136	30	28				1
*	<i>Rumex crispus</i>	31	44	13	6	1			1
1	<i>Salix interior</i>	10	8	9	7	14	27	25	20
*	<i>Setaria faberi</i>	116	11	1					
*	<i>S. glauca</i>	299	38	4	2				
*	<i>S. viridis</i>	137	113	4	2				
5	<i>Silphium integrifolium</i>								10
5	<i>S. laciniatum</i>	192	196	161	173	209	171	203	323
5	<i>S. perfoliatum</i>	19	18	28	13	9	6	1	7
5	<i>S. terebinthinaceum</i>					2	2	1	2
0	<i>Solanum americanum</i>	15		3					
1	<i>Solidago altissima</i>	7	2	15	56	98	59	51	59
4	<i>S. rigida</i>	77	96	165	185	238	359	299	356
*	<i>Sonchus uliginosus</i>	10	48	1	1				
5	<i>Sorghastrum nutans</i>	24	41	51	58	52	56	83	45
4	<i>Spartina pectinata</i>	7	9	8	7	13	15	20	23
10	<i>Sporobolus heterolepis</i>	1	2	1	1	5	7	7	3
*	<i>Taraxacum officinale</i>	309	145	119	19	13	4		
*	<i>Trifolium hybridum</i>	37	47	9	5	5	16	1	
*	<i>T. pratense</i>	52	31	90	1				
5	<i>Vernonia fasciculata</i>					1			
7	<i>Veronicastrum virginicum</i>							1	2
*	<i>Xanthium americanum</i>	1	1						
T	(Total C)	131	138	140	141	149	145	160	183
N ₁	(Number of Species)	72	72	66	50	43	42	35	46
N ₂	(Number of Native Species)	38	39	39	31	29	29	31	37
C	(Mean C Value)	3.28	3.54	3.59	4.55	5.14	5.00	5.16	4.95
IV	(Index Value)	20.74	22.11	22.42	25.33	27.09	26.93	28.74	30.11

4). The following "troublesome" weed species, listed with number of individuals (Table 4) still present in the seed broadcast area, include: wild carrot (*Daucus carota* L.) 8, sweet clovers (*Melilotus* spp.) 19, Kentucky bluegrass (*Poa pratensis* L.) 26, sandbar willow (*Salix interior* Rowlee) 20, and tall goldenrod (*Solidago altissima* L.) 59. Of these species and for this prairie, white and yellow sweet clover, sandbar willow and tall goldenrod appear to be the greatest weed threats.

Five prairie plant species ($C \geq 4$) were not found growing in 1999 (Table 4). These species were heath aster (*Aster ericoides* L.), New England aster (*A. novae-angliae* L.), wild quinine (*Parthenium integrifolium* L.), marsh cress (*Rorippa palustris* (L.) Besser fernaldiana (Butters & Abbe) Stuckey) and common ironweed (*Vernonia fasciculata* Michx.). Of these five species, only wild quinine was knowingly in the original seed broadcast mixture.

The population of compass plant (*Silphium laciniatum* L.) increased

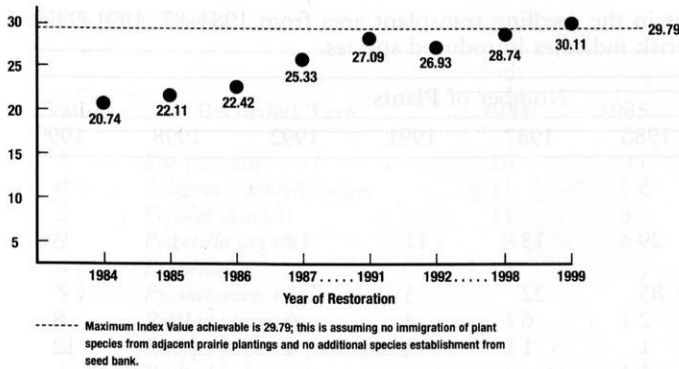


Fig. 2. Index Value of seed broadcast area.

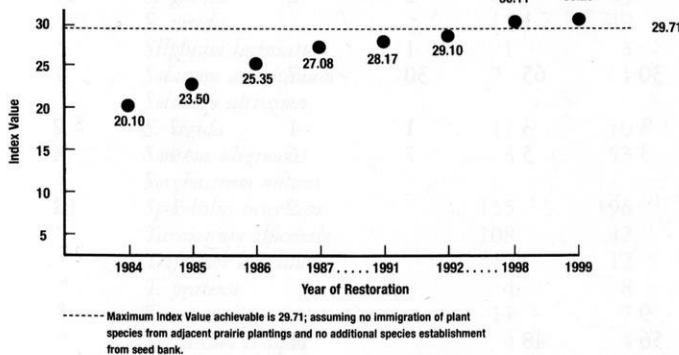


Fig. 3. Index Value of seedling transplant area.

from 196 to 323. With the exception of wild bergamot (8 individuals) and rosinweed (10 individuals), the other species that invaded the seed broadcast area have four or fewer individuals. According to Betz et al. (1995), showy tick trefoil, wild bergamot, switchgrass, foxglove beard tongue, and rosinweed are species of Stage 1 of the prairie matrix.

Seedling Transplant Area

Table 5 lists the plant species found growing in the seedling transplant area from 1984 to 1999. During 1999, 22 prairie species with a numerical rating of 4 or above were present in the seedling transplant sample area. Of these 22 species, big bluestem (*Andropogon gerardii* Vitman), side-oats grama (*Bouteloua curtipendula* (Michx.) Torr.), tall coreopsis (*Coreopsis tripteris* L.), yellow coneflower (*Ratibida pinnata* (Vent.) Barnhardt), Indian grass (*Sorghastrum nutans* (L.) Nash), heath aster, showy tick trefoil, switchgrass, foxglove beard tongue, and compass plant germinated from the adjacent seed broadcast site and other subsequent planting areas. The population of compass plants increased from 3 to 33. The seedlings were planted one foot apart; their survival and mortality was not recorded. Spaces freed by plant mortality probably allowed for these additional species to become established. From 1984 to 1999, the IV increased from 20.10 to 30.20 (Fig. 3). The maximum IV that the seedling transplant area could achieve is 29.71 (Table 2) without immigration of species from adjacent plantings. It was unlikely that any prairie seeds were present in the clay and rubble subsoil.

Six prairie plant species ($C \geq 4$) were not found growing in 1999 (Table 5). These species were smooth blue aster (*Aster laevis* L.), com-

mon mountain mint (*Pycnanthemum virginianum* (L.) T. Durand & B. D. Jacks.), hoary vervain (*Verbena stricta* Vent.), heath aster, prairie blazing star, and marsh cress. Of these six species, only prairie blazing star and hoary vervain were planted as seedlings.

Fifty-one weed species, native species with $C < 4$ and introduced species, disappeared from the seedling transplant area (Table 5). The IV increase and decrease of weed species indicated that the seedling transplant area has also been progressing toward prairie. The following weed species that appear to be becoming established, along with their number of individuals in the sampled area (Table 5), were tall goldenrod, 19, and sweet clovers, 42.

Analysis of Seed Broadcast and Seedling Transplant Areas

There was a slow but steady decline of weed species and consistent increase in coverage of native prairie species for both the seed broadcast and seedling transplant areas during the first 16 years of assessment. Weeds occurred spontaneously from the 7–10 cm of black soil used to top-dress the area, from the clay and rubble subsoil, from the adjacent marsh vegetation area, and from the oat and wheat straw mulch that was scattered on both the broadcast and transplant areas.

There was no weed removal in these areas; burning began on an annual basis in 1988. It appears that burning was at least partly responsible for eliminating 49 weed species in the seed broadcast area (Table 4) and 51 weed species in the seedling transplant area (Table 5). Sweet clovers and tall goldenrod were the only weed species establishing themselves in the interior of the prairie. Other weeds still present in both sites are growing along the periphery or in disturbed areas.

The number of individual plants of prairie grasses has evidently not increased due to the annual springtime fires that began in 1988. In the seedling transplant area, big bluestem increased from 5 plants in 1985 to 12 in 1999. Five individuals of Indian grass were counted in 1999, none in 1985 (Table 5). In the seed broadcast area, big bluestem decreased from 791 plants in 1985 to 658 in 1999. Indian grass individuals increased from 41 plants in 1985 to 45 in 1999 (Table 4).

From 1985 to 1999, most populations of prairie forbs remained the same or increased in the sampled areas. For example, the population of compass plants increased greatly in both areas; 3 to 33 in the seedling transplant area and 196 to 323 in the seed broadcast area. Compass plant thrives in this site's clay and rubble subsoil.

Declines in the seedling transplant area were observed for pale purple coneflower (*Echinacea pallida* Nutt.), 16 to 12, rattlesnake master (*Eryngium yuccifolium* Michx.), 9 to 6, prairie blazing star, 8 to 0, and wild quinine, 4 to 1 (Table 5). Notable declines in the seed broadcast area were observed for pale purple coneflower, 103 to 21, and wild quinine, 4 to 0 (Table 4). Most of this decline is due to meadow vole (*Microtus pennsylvanicus* Ord.) herbivory; numerous vole burrows and vole destruction of plant underground storage organs, such as corms, have been observed during all 16 years in this reconstruction.

Discussions and conclusions drawn from this data may be applicable to future prairie planting assessments on clay and rubble subsoil with a minimum of black top soil. The performance standard of a reconstruction project probably will not be higher than species planted, especially on clay and rubble subsoil. There was no significant difference ($P > 0.05$) in the quality of prairie reconstruction between seed broadcast and seedling transplant methods. To predict species success at a similar site, the species planted should be the same or, at least, have the same average conservative values.

Table 5. Assignment of C values and abundance of plant species in the seedling transplant area from 1984–87, 1991–92, and 1988–99. Nomenclature is from Swink and Wilhelm (1994). Asterisk indicates introduced species.

C Value	Recorded Taxa	Number of Plants							
		1984	1985	1986	1987	1991	1992	1998	1999
*	<i>Abutilon theophrasti</i>	21	40	3					
0	<i>Acalypha rhomboidea</i>		1						
*	<i>Agropyron repens</i>	7	31	29	13	11	12	1	3
*	<i>Amaranthus retroflexus</i>	8							
0	<i>Ambrosia artemisiifolia</i>	23	428	85	22	3	3		
9	<i>Amorpha canescens</i>		3	2	6	4	6	10	8
5	<i>Andropogon gerardii</i>	3	5	1	1	3	4	5	12
*	<i>Anthemis cotula</i>			1					
*	<i>Arctium minus</i>	1	3	2	4				
*	<i>Atriplex patula</i>	3	5						
0	<i>Asclepias syriaca</i>								1
5	<i>Aster ericoides</i>					2	2	9	16
4	<i>Aster novae-angliae</i>				1				
9	<i>Aster laevis</i>					1			
0	<i>A. pilosus</i>		4	30	65	30	7		
*	<i>Avena sativa</i>	59							
8	<i>Baptisia leucantha</i>		3	3	3	1	1	2	2
10	<i>B. leucophaea</i>		1	3	5	7	6	4	4
*	<i>Barbarea vulgaris</i>	14	1						
8	<i>Bouteloua curtipendula</i>						2	1	2
0	<i>Brassica kaber</i>	5	1						
*	<i>Cerastium vulgatum</i>	8							
*	<i>Chenopodium album</i>	89	17						
*	<i>Cichorium intybus</i>		8	9					
*	<i>Cirsium arvense</i>	9	16	56	48		1		
*	<i>C. vulgare</i>	1	9	46	14				
6	<i>Coreopsis palmata</i>	3	10	17	24	36	41	60	55
5	<i>C. tripteris</i>		1	1	1		1	1	3
1	<i>Cyperus strigosus</i>	26							
*	<i>Dactylis glomerata</i>	1							
*	<i>Daucus carota</i>	8	16	267	122	3	6		
4	<i>Desmodium canadense</i>								1
8	<i>Echinacea pallida</i>	9	16	56	48		1	10	12
0	<i>Echinochloa crusgalli</i>	36	2						
0	<i>Erigeron canadensis</i>		9	6	2				
9	<i>Eryngium yuccifolium</i>	7	9	5	6	4	4	4	6
0	<i>Euphorbia supina</i>	5							
*	<i>Festuca elatior</i>	3	2	3	1				
2	<i>Helianthus grosseserratus</i>	3							
*	<i>Hibiscus trionum</i>	10	14	3					
*	<i>Hordeum jubatum</i>		5	23	9				
*	<i>Lactuca serriola</i>		1						
0	<i>Lepidium virginicum</i>	1	2	2					
8	<i>Liatris pycnostachya</i>		8	1	2				
*	<i>Lychnis alba</i>				1				
*	<i>Medicago lupulina</i>					1		2	4
*	<i>Melilotus spp.</i>	1	1	1		3	2		5
0	<i>Oxalis stricta</i>	1	4	4					
0	<i>Oenothera biennis</i>			3	4				
5	<i>Panicum virgatum</i>								1
8	<i>Parthenium integrifolium</i>	7	4	6	5	3	3	1	1
4	<i>Penstemon digitalis</i>		2	2	1		2		1
9	<i>Petalostemum candidum</i>	14	15	18	26	31	45	10	8
9	<i>P. purpureum</i>	6	14	18	23	46	41	55	52
*	<i>Pbleum pratense</i>			1					
0	<i>Physalis subglabrata</i>					1	2		
*	<i>Plantago major</i>	8	14	6	18	1			
0	<i>P. rugelii</i>	2	3						

Table 5. Continued.

C Value	Recorded Taxa	Number of Plants							
		1984	1985	1986	1987	1991	1992	1998	1999
*	<i>Poa pratensis</i>	10	9	4		12	10	6	1
0	<i>Polygonum pensylvanicum</i>	11	5						
2	<i>Populus deltoides</i>	11	3	3	1				
9	<i>Potentilla arguta</i>	8	6	6	7	10	10	8	6
0	<i>P. norvegica</i>	3	2	2					
5	<i>Pycnanthemum virginianum</i>						1		
4	<i>Ratibida pinnata</i>	3	1		13	10		8	7
4	<i>Rorippa palustris fernaldiana</i>	2							
1	<i>Rudbeckia hirta</i>	1	1	13	4				
*	<i>Rumex crispus</i>	6	6	8	7		1		
1	<i>Salix interior</i>					1	1	1	2
*	<i>Setaria faberi</i>	19		2					
*	<i>S. glauca</i>	61	33	6					
*	<i>S. viridis</i>	15	49	12	1				
5	<i>Silphium laciniatum</i>	1	3	1	1	9	14	26	33
0	<i>Solanum americanum</i>	7	1						
1	<i>Solidago altissima</i>			10	11	16	17	25	19
4	<i>S. rigida</i>	17	10	29	45	79	120	69	85
*	<i>Sonchus uliginosus</i>	3	53	15					
5	<i>Sorghastrum nutans</i>					1	2	4	5
10	<i>Sporobolus heterolepis</i>	155	196	203	189	188	188	172	163
*	<i>Taraxacum officinale</i>	108	42	79	7	1	5		
*	<i>Trifolium hybridum</i>	12	12	8	2		6		
*	<i>T. pratense</i>	4	8	4	2				
*	<i>T. repens</i>	11	7	58	9				
*	<i>Verbascum thaspus</i>	4	4	2	1				
4	<i>Verbena stricta</i>	1	1	1	1	1	2		
*	<i>Xanthium americanum</i>				2				
T	(Total C)	110	137	134	138	138	151	138	151
N ₁	(Number of Species)	54	58	52	42	31	35	24	29
N ₂	(Number of Native Species)	29	34	28	26	24	27	21	25
C	(Mean C Value)	3.67	4.03	4.79	5.31	5.75	5.60	6.57	6.04
IV	(Index Value)	20.10	23.50	25.35	27.08	28.10	29.10	30.11	30.20

Seeds of *Andropogon gerardii*, *Coreopsis tripteris*, *Ratibida pinnata*, *Rudbeckia hirta*, and *Silphium laciniatum* from seed broadcast mixture became established in seedling transplant area

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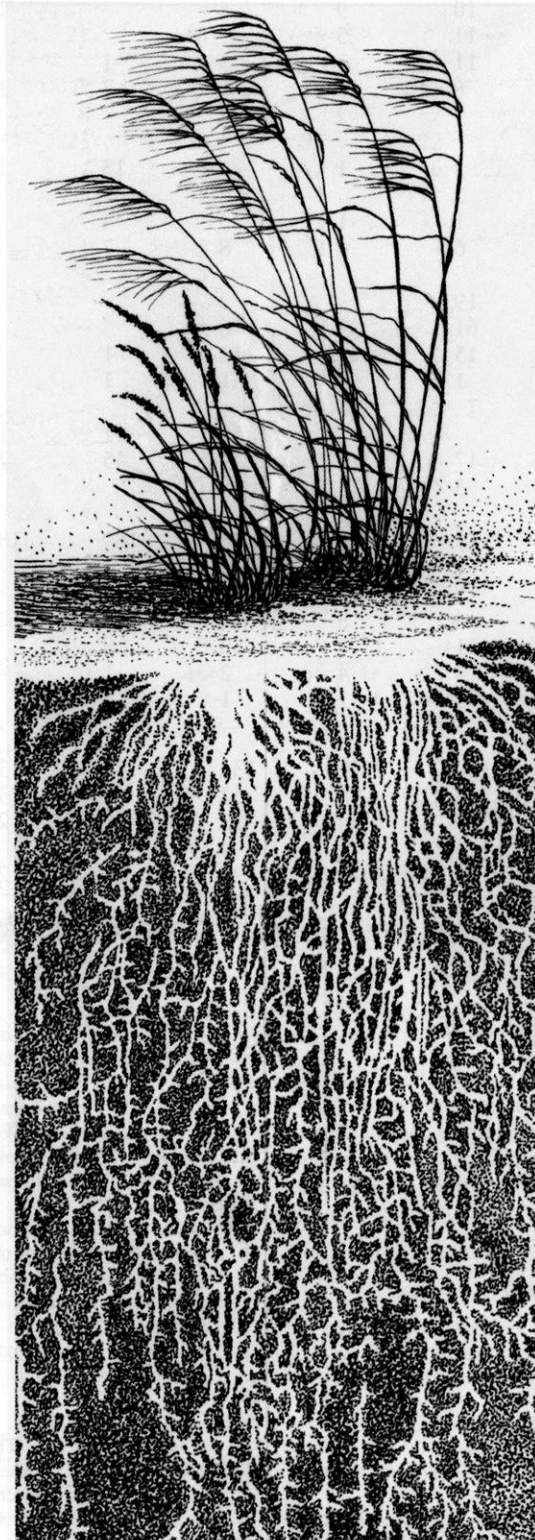
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Microbial Biomass and Activity in Soils from Virgin Prairies Compared with Prairie Restoration, Forest and Agricultural Sites in Illinois

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Little is known about the communities of free-living (asymbiotic) microbial communities inhabiting prairie soils. In this study, total viable microbial biomass (from phospholipids), culturable asymbiotic nitrogen-fixers, and Biolog metabolic profiles were compared in soils from a prairie restoration, a soybean field, a forest and three virgin prairie remnants. The virgin prairies consistently had much greater total viable biomass than the prairie restoration or an agricultural field planted in soybeans, but the soybean field had a higher count of free-living nitrogen-fixing bacteria. Viable microbial biomass correlated positively with soil organic content. Except for the agricultural field, the top 1 cm of soil had more biomass per gram of soil than the 5-7 cm depth. Rates of carbon substrate metabolism also differed significantly in the different treatments, as shown by a discriminant analysis. The prairie restoration soil also showed significantly less diversity in the substrates metabolized by the microbiota, and for those substrates in which metabolic rates differed between sites, the virgin prairies always had higher rates than the corresponding restoration or agricultural site. We conclude that the conversion of farmland into prairie may significantly improve the biomass and activity of the soil microbial communities, but it may take decades or longer to approach the levels found in a virgin prairie. Eventually, we hope to be able to predict this progress and to determine the effects of these changes on the rates of soil processes.

INDEX DESCRIPTORS: soil, bacteria, microbes, microbial biomass, microbial metabolism, asymbiotic nitrogen-fixers, organic matter, Biolog, community-level physiological profiles (CLPP), CLPP, substrate utilization, prairie restorations, agriculture, flatwood forest, virgin prairie, mesic prairie.

Prior to European settlement, 8,900,000 ha of Illinois were tallgrass prairie (Samson and Knopf 1994). More than 99.9% of the original tallgrass prairie of Illinois has been lost to the plow (Noss et al. 1999), with only about 930 ha of prairie remaining. Although the impact of farming on plant species composition, biomass and diversity is obvious, the impact on the soil communities is less apparent and more difficult to study directly.

Soil microorganisms (bacteria, fungi, protozoa and algae) play vital roles in maintaining the health and integrity of the soil itself as well as helping to maintain the health of the plant and animal communities. Although some symbiotic microorganisms (e.g., mycorrhizae, *Rhizobium*, etc.) interact specifically with particular species of plants or animals, most microorganisms in the soil are free-living or can associate in a less specific and obligate manner with macroorganisms. These free-living microbes are essential to terrestrial ecosystems, carrying out many metabolic activities key to decomposition processes and biogeochemical cycles that return nutrients and organic matter to the soil. Nitrogen fixation, for example, has been called the second most important biological process on Earth after photosynthesis (Graham 2000), and asymbiotic nitrogen fixation has been found to be the principle source of biologically-fixed nitrogen in tallgrass prairies (Kapusta 1980). Nitrogen has been proposed as the nutrient having the most importance in limiting and structuring tallgrass prairie ecosystems (Blair et al. 1998). Carbon cycling and sequestration are also mediated by microorganisms. It has been shown that cultivation has significant effects on these rates and ultimately results in loss of soil organic matter to the atmosphere as carbon dioxide (Tiessen et al. 1982, Elliot 1986, Dick 1992, Wander and Bollero 1999).

Soil microorganisms also modify the soil structure, affecting such

properties as aggregation, water holding capacity, wetability and porosity. Microbial biomass, diversity and activity are often listed as important indicators of soil health and quality (Pankhurst 1997, Roper and Ophel-Keller 1997, Singer and Ewing 1997, Sparling 1997, White and Macnaughton 1997), in addition to such characteristics as soil organic matter, texture, pH, bulk density and other physical-chemical properties. However, it has been estimated that less than 10% of all microbes in nature (including soils) are culturable (Winding et al. 1994, Palojarvi et al. 1997), and, therefore, microbial communities cannot be characterized solely by methods that rely upon growing the organisms in the laboratory.

The goals of this study were to (1) assess a set of microbial methods for use in monitoring soil microbial communities during prairie restorations and (2) determine the effects of prairie restoration on microbial soil communities and other soil parameters. We hypothesized that the soils from the prairie restorations would exhibit some signs of recovery from disturbance by having soil and microbial characteristics intermediate between those in the agricultural site and the virgin prairie sites. The years of lack of tillage and increased plant diversity should allow the soil microbial communities to increase in biomass and functional diversity.

We compared the microbial communities in the surface layers of soils from a virgin prairie, an adjacent prairie restoration, and an adjacent forest in Cook County, IL, as well as another nearby high-quality virgin prairie site. Also, a virgin prairie was compared with an adjacent agricultural field at a railroad remnant site in McHenry County, IL. In each case, the microbial communities were characterized by measuring the total viable microbial biomass (as phospholipid phosphate), numbers of culturable asymbiotic N₂-fixing bacteria (heterotrophic diazotrophs), and community substrate utiliza-

Table 1. Soil texture data for the sites sampled (top 5 cm of soil, means of five replicate samples at each site), site codes and dates of sampling.

Site Sampled	Code	Date	Texture	% Sand	% Silt	% Clay
James Woodworth Virgin Prairie	JWV	24 June	Loamy sand	82	10.5	7.5
Bunker Hill Virgin Prairie	BHV	8 July	Sandy loam	77	16	7
Bunker Hill Prairie Restoration	BHR	15 July	Sandy loam	56	30	14
Bunker Hill Forest	BHF	15 July	Loam	51	39	10
Huntley Virgin Prairie	HV	5 August	Sandy loam	65	27	8
Huntley Agricultural Field	HA	5 August	Sandy loam	65	22	13

Table 2. Soil environmental characterization for each of the sites sampled (see Table 1 for site codes). Samples of surface soils (top = 0–1 cm depth) and slightly deeper soils (bottom = 5–7 cm depth) were taken from the same cores (nd = no data). Values are means \pm standard deviations ($n = 5$).

Site	Depth	Temp. (°C)	Organics (%)	Moisture (%)	pH
JWV	top	31.2 \pm 2.8	18.63 \pm 0.57	10.98 \pm 1.75	7.16 \pm 0.20
	bottom	26.2 \pm 2.4	17.36 \pm 0.37	21.98 \pm 1.54	6.96 \pm 0.19
BHV	top	20.6 \pm 1.2	7.72 \pm 0.55	19.28 \pm 2.00	6.64 \pm 0.08
	bottom	19.7 \pm 0.5	5.81 \pm 0.39	17.17 \pm 0.93	6.62 \pm 0.11
BHR	top	26.6 \pm 0.4	7.94 \pm 0.80	6.34 \pm 1.07	6.38 \pm 0.24
	bottom	26.0 \pm 0.3	5.27 \pm 0.79	10.10 \pm 1.03	6.24 \pm 0.27
BHF	top	25.3 \pm 0.3	8.21 \pm 1.16	15.70 \pm 1.88	6.63 \pm 0.26
	bottom	24.5 \pm 0.2	6.04 \pm 0.36	13.87 \pm 1.56	6.22 \pm 0.32
HV	top	21.7 \pm 0.3	9.52 \pm 1.82	25.13 \pm 3.95	7.98 \pm 0.23
	bottom	21.4 \pm 0.2	6.25 \pm 1.39	17.36 \pm 5.68	8.12 \pm 0.20
HA	top	22.2 \pm 0.2	3.78 \pm 0.23	21.10 \pm 1.01	5.88 \pm 0.88
	bottom	22.0 \pm 0.1	nd	26.32 \pm 4.75	5.98 \pm 0.99

tion patterns (community-level physiological profiles, or CLPPs) using the Biolog GN assay. This information will help us to determine whether prairie restorations improve soil microbial diversity and function and soil quality.

METHODS

Site Descriptions

Soils were sampled from three separate locations in northeastern Illinois, and in two of these cases, more than one ecosystem (site) was sampled in a given location. Table 1 lists the sites in the order that they were sampled in the summer of 1995, along with soil texture data. Table 2 details the general soil environmental conditions (temperature, moisture, organic matter and pH) at each of the soil sampling sites and depths.

The James Woodworth Prairie Preserve (also known as Peacock Prairie, after the original homesteader) is a 2.1 ha tallgrass prairie remnant which is now surrounded by urban commercial and residential development. The Preserve is owned and managed by the University of Illinois at Chicago (UIC) and is located northwest of Chicago on the edge of the city of Niles, Maine Township, Cook County, IL, on the east side of Milwaukee Avenue 0.8 km (0.5 mi.) north of the intersection with Golf Road. Numerous studies have been conducted in the preserve on the insect communities (Paintin 1929, Auerbach 1951, Park et al. 1953, Hamilton 1981) and plant communities (Betz and Cole 1969, Apfelbaum and Rouffa 1981, Apfelbaum and Rouffa 1982). The area sampled during this study (site JWV) is mesic "virgin" tallgrass prairie (Albert S. Rouffa, pers. comm.) with little or no soil disturbance. Over 200 plant species have been identified in this area, showing a high degree of native plant species richness (Apfelbaum and Rouffa 1982). The area sam-

pled is just east of the path leading through the prairie from the Interpretation Center in approximately the center of the eastern half of the property. The soils here are typical Mollisols of black-soil prairie, containing a thick horizon of organic-rich, dark soil in the root zone and having a hue of 5YR, value of 2.5, and chroma of 1 for dry soil using the Munsell Soil Color Chart for comparison (Munsell Color 1994).

Bunker Hill Prairie (3.2 ha) and Edgebrook Flatwoods (31.6 ha) are adjacent areas which are listed in the Illinois Natural Areas Inventory, owned by the Forest Preserve District of Cook County, and managed together by the North Branch Prairie Project and the Volunteer Stewardship Network of The Nature Conservancy (North Branch Prairie Project 1990, 1994). Bunker Hill Prairie is on the northwestern edge of the city of Chicago, near Niles, IL, and about 6 km (3.75 miles) south and 5 km (3.1 miles) east of the James Woodworth Prairie Preserve. The prairie and forest areas sampled are located in a triangle bordered by Devon Avenue on the south, Caldwell Avenue on the northeast, and the North Branch of the Chicago River on the west. The prairie area is a wet to wet mesic prairie/oak opening that may have standing water in spring but is very dry by midsummer (North Branch Prairie Project 1990). Three different sites were sampled at Bunker Hill. One prairie site (BHV) is believed to be undisturbed in terms of the soil profile, so it is considered "virgin prairie" for the purposes of this study. It may have been grazed, and it was mowed as a play area in the past (stewards Jane and John Balaban, personal communication). An adjacent prairie site (BHR) has soils that were disturbed in the past by farming but is currently being managed as a prairie restoration. Restoration began at Bunker Hill (BHR) in 1983, including burning sections of the prairie each year from 1984 until 1994. The adjacent flatwoods site (BHF) is second growth forest and lies just east of the north branch

of a creek that drains into the river. As with most Cook County Forest Preserves, these woods are heavily foraged by deer. The topography at Bunker Hill is flat, with clayey, hardpan soil that is slowly permeable. None of the Bunker Hill soils were as dark in color as the soil from the James Woodworth Prairie. The forest soil (BHF) was the darkest in color (Munsell color 10YR, 3.5/1), with the virgin prairie (BHV) having a Munsell color of 5 to 7.5YR, 5/1 and the restoration soil (BHR) having a Munsell color of 10YR 4.5/2 for dry soil. The restoration soil seemed to be more compacted and was much harder to core than the other two sites.

The third location sampled is a railroad-associated prairie remnant (site HV) near Huntley in McHenry County, IL, approximately 72 km (45 miles) west-northwest of Chicago on the border between Grafton and Coral townships. The site is located on the west side of the main tracks of the Chicago and Northwestern R.R. (formerly the Huntley-Union-Marengo R.R.) between Huntley and Union, IL. This high-quality wet mesic virgin tallgrass prairie remnant (HV) is an Illinois Nature Preserve and is managed by the McHenry County Conservation District. A soybean field (site HA) west of the prairie, and separated from it by a set of siding tracks, was also sampled for comparison. The prairie remnant had rich, dark soil (Munsell color 10YR 4/1 for dry soil) while the adjacent farmland soil had a lighter, reddish color, was more cloddy and very clayey in feel. Because it had rained recently, the farm soil was so dense and sticky that it could not be sieved.

Soil Sampling

Soils at each location were sampled in the morning and immediately returned to the laboratory for analysis. Five randomly chosen replicate areas were sampled within each of the six sites (30 total soil samples), but areas in unrepresentative small topographic depressions or mounds were avoided. Samples were taken between plants, avoiding as many roots as possible. Soil was extracted from the ground using small corers (2.2 cm diameter, 11 cm long cork borers), with enough cores taken from each replicate area to fill a small, sterile Whirl-Pak (Nasco, Fort Atkinson, WI.) bag $\frac{3}{4}$ full (to the 4 oz fill line). The corers were marked at measured intervals, and the soil from a depth of 5–7 cm (the bottom of the core) was analyzed separately from the soil from a depth of 0–1 cm (the top of the core).

Samples were immediately placed into a cooler containing ice packs, but the soil bags were not allowed to come in direct contact with the ice in an attempt to keep the microorganisms cool but not frozen. When all five of the replicates had been taken from a given site, the soil samples were sieved through a wire mesh with square openings that were 2 mm on each side, and stones, insects and roots were removed. Five grams of sieved soil were removed for lipid extraction, and the remainder of the sample was placed in sterile plastic Whirl-Pak bags and returned to the laboratory in the cooler. All sampling and sieving gear was cleaned, but not sterilized, between samples. Sampling and sieving were carried out as quickly as possible in order to minimize changes in the soil microbial communities prior to analysis. In general, it took about one hour to take and sieve the five replicate samples from each site, and the samples arrived in the laboratory no more than four hours after the start of sampling.

Soil Analysis

As soon as the soil samples arrived in the laboratory, microbiological analyses were begun on subsamples of each replicate, and the remainder was stored at 4°C until further analysis. Within the week, moisture content was determined by drying weighed samples at 80°C ($\pm 1^\circ\text{C}$) overnight to constant weight and reweighing (± 0.01 g). The dried samples were then ashed in a muffle oven at 350°C

($\pm 5^\circ\text{C}$) overnight and reweighed to determine the percentage organic matter (ash-free dry weight; Brower et al. 1997).

Soil texture was determined by a modified hydrometer method (Cox 1990, Brower et al. 1997). Fifty grams of sieved, oven-dried soil were stirred together with 100 ml of 5% sodium hexametaphosphate for two hours. The suspension was then combined with 400 ml of distilled water in a Waring blender and mixed for two 1-minute cycles at low speed. The suspension was then rinsed into a 1000 ml graduate and brought up to 1000 ml with distilled water. The cylinder was covered, mixed gently by inverting 30 times, and placed on a flat surface. Hydrometer and temperature readings were taken at 40 sec, 60 sec, 2 min, 5 min, 15 min, 30 min, 1 h, 2 h, 4 h, 6 or 8 h, and 24 h after mixing. A blank cylinder was made up with no soil to obtain temperature correction factors. For each time, the maximum particle diameter in solution was plotted against the % soil particles less than that diameter remaining in solution (Brower et al. 1997), and from the smoothed curve, the percent sand ($\geq 50 \mu\text{m}$), silt ($< 50 \mu\text{m}$ but $> 2 \mu\text{m}$) and clay ($\leq 2 \mu\text{m}$) were determined.

Microbial Biomass

Microbial biomass was determined as the amount of extractable phospholipid phosphate per gram of dry soil, which gives a good estimate of the total viable microbial biomass because phospholipids have been shown to break down rapidly after cell death (White et al. 1979). Total lipids were quantitatively extracted from sieved soil samples in the field immediately after sampling (Bligh and Dyer 1959, White et al. 1979). In the field, 5 grams of soil were mixed with 20 ml of methanol and 10 ml of chloroform in a glass jar having a Teflon-lined lid, and the jars were returned to the laboratory. Up to one week later, the soil extracts were quantitatively transferred to 50 ml Teflon Oak Ridge tubes and centrifuged at $3000 \times g$ for five minutes. The supernatants were transferred to 60 ml separatory funnels, and the soil dry weight was determined from the dried pellet. To each separatory funnel was added an additional five ml of chloroform and 15 ml of distilled water, giving a ratio of water/methanol/chloroform of 0.9:1:1 (V/V/V). The funnels were shaken, the mixtures allowed to separate overnight, and the organic phase was collected from the bottom layer. The solvent was removed in a rotary evaporator at 35°C, the concentrated samples were resuspended in 2–4 ml of chloroform, transferred to glass test tubes having Teflon-lined caps, dried under a stream of nitrogen gas at 35°C, and stored at -20°C until analysis. Prior to analysis, the samples were resuspended in 5.00 ml of chloroform, and 500 μL aliquots were placed into 16 mm \times 15 cm acid-washed test tubes (HCl : distilled water (1:1, vol/vol)). All of the chloroform was removed under a stream of nitrogen prior to the addition of 1.5 ml of 23% perchloric acid. In order to oxidize the lipids and leave only inorganic phosphate, samples were refluxed with the acid in a 180°C heating block at a 45° angle in a perchloric acid fume hood until colorless (about 2 hours) but were not allowed to become dry. After cooling, 2.4 ml of molybdate reagent (4.4 g ammonium molybdate, 14 ml concentrated H_2SO_4 per L distilled water) and 2.4 ml of Fiske & Subbarow reducer (Sigma) were added. After 10 min in a boiling water bath, the blue color was measured at the absorption maximum of 830 nm on a Spectronic 20. A standard curve ($r^2 = 0.997$) was constructed using known phosphate concentrations.

Asymbiotic nitrogen fixing bacteria

Within two to four days of sampling, soils were plated onto a nitrogen-free medium to get plate counts of nitrogen-fixing bacteria. One gram of sieved soil was shaken vigorously in 99 ml of sterile distilled water for two min, followed by serial dilution. Then 0.1 ml

aliquots of the 10^{-3} , 10^{-4} , and 10^{-5} dilutions were plated onto Winogradsky agar plates (Bergey's Manual 1984) containing 1% glucose, giving final dilutions of 10^{-4} , 10^{-5} , and 10^{-6} , respectively. Plates were incubated at 25°C for three days prior to counting.

Substrate Utilization Profiles

Immediately after the samples arrived in the laboratory, portions of each sample were prepared for inoculation into Biolog GN[®] microtiter plates (Biolog, Inc., Hayward, CA). These commercially-prepared plates consist of 95 wells, each containing a different sole carbon source, nutrients, and the redox indicator dye tetrazolium violet which detects respiration as the formation of NADH. The 96th well is a blank containing no carbon source. The range of substrates includes 28 carbohydrates, 24 carboxylic acids, 20 amino acids, 4 additional aromatic compounds, 5 polymers, 3 amides, 3 amines, 3 phosphorylated compounds, 2 esters, 2 alcohols and a brominated compound, all of which have been described previously (Garland and Mills 1991).

Ten grams (± 0.01 g) of sieved soil were added to 50 ml of sterile 54 mM phosphate buffer (pH 7.0) in a square dilution bottle and shaken vigorously for 30 sec. To promote settling of soil particles, 5 mg each of magnesium carbonate and calcium chloride were added, the bottles shaken for 15 sec, and then allowed to settle for 10 minutes. After settling, 20 ml of the suspension was pipetted into an empty sterile bottle. Using a Spec 20 spectrophotometer at 590 nm, the OD of the suspension was adjusted to 0.45 (± 0.01) using sterile phosphate buffer.

After all of the replicate samples were adjusted to the same OD, 150 μ L was pipetted into each well of the microtiter plates using a multi-channel pipettor. Two replicate plates were inoculated for each of the five replicate soil samples (except for JWV, for which three replicate plates were inoculated for each soil sample). Incubation times were kept as short as possible in order to minimize the effects of growth and population shifts in the wells. After 24 and 48 hours of incubation at 27°C, plates were read by eye from below against fluorescent lights using a scale of 0–4 to record the density of blue dye formation in each well. A standard template for comparison with each plate was made using blue markers on clear plastic. A score of 0 indicated no visible blue color, 1 indicated detectable but very pale blue, and 4 indicated very dark blue to black. When totaling the number of substrates utilized by each sample, only readings greater than one were counted as "positive". A modified Shannon Diversity Index, H' , was calculated based upon the utilization of substrates by each sample as follows: $H' = -\sum p_i(\ln p_i)$, where p_i is the ratio of the intensity of utilization of a particular substrate (absorbance or relative intensity of dye formation) to the sum of the intensities of all of the 95 substrates (Zak et al. 1994).

Statistics

Data were entered and transformed in Microsoft Excel, and statistical analyses were conducted in Statistica '99 (StatSoft, Inc., Tulsa, OK). Bacterial colony counts were log transformed. Pairwise comparisons of soil organics, biomass and colony counts were made using Tukey's HSD test following an ANOVA, correlations were calculated using Pearson's r , and multi-way comparisons were made using the non-parametric Kruskal-Wallis test. A principal components analysis (PCA) with a biqartimax normalized rotation was used to select the Biolog substrates that most explained the variance between samples. Substrates selected in the PCA were entered into a stepwise discriminant analysis (DA) to test the hypothesis that microbial substrate utilization could allow one to discriminate between sites (ecosystems).

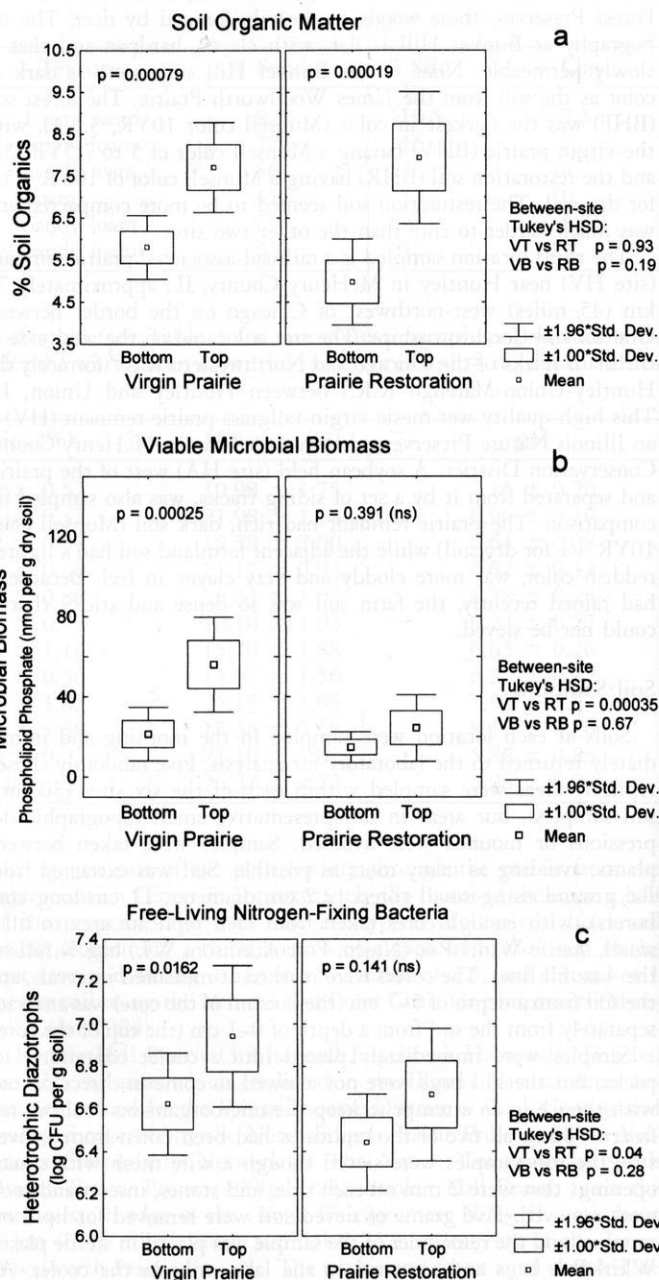


Fig. 1 Bunker Hill Prairie soil (a) organic matter, (b) viable microbial biomass, and (c) free-living nitrogen-fixing bacteria in a virgin prairie (site BHV) and an adjacent 12-year prairie restoration (site BHR). The "Bottom" of the core was 5–7 cm below the soil surface, and the "Top" of the core was 0 to 1 cm from the surface. Values shown are the means \pm one and 1.96 Std. Dev. for five replicate samples at each site; P values are for post hoc tests (Tukey's HSD) following an ANOVA.

RESULTS

Organic Matter, Microbial Biomass and Nitrogen-fixers

There were significant differences between these ecosystems in the soil characteristics and in the soil microbial communities (Figs. 1 and 2). The virgin prairie soils at JWV contained more organic matter than any of the other sites (Table 2). The differences in or-

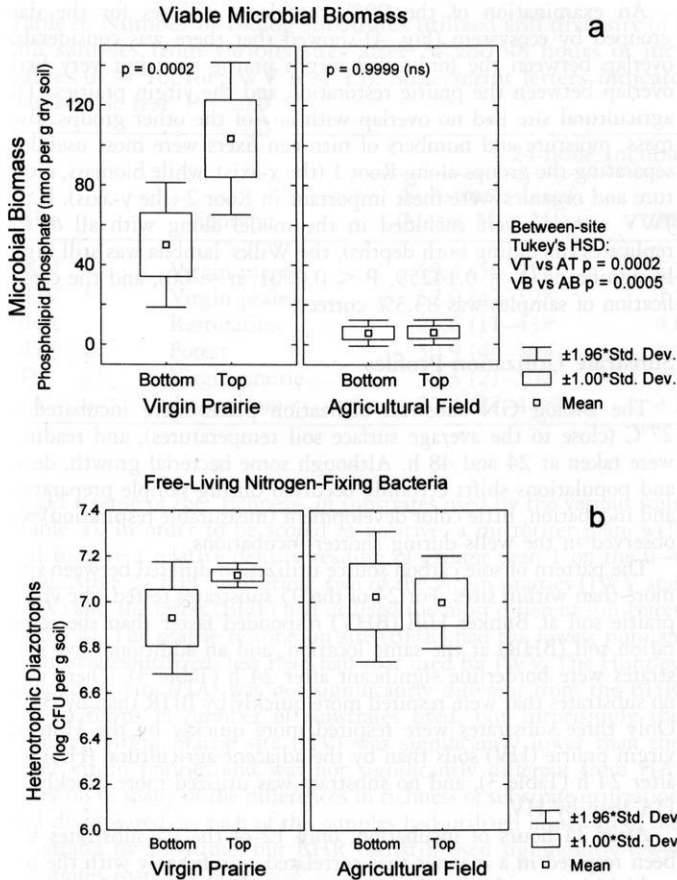


Fig. 2 Huntley railroad remnant prairie soil (a) viable microbial biomass, and (b) free-living nitrogen-fixing bacteria in a virgin prairie (site HV) and an adjacent soybean field (site HA). The "Bottom" of the core was 5–7 cm below the soil surface, and the "Top" of the core was 0 to 1 cm from the surface. Values shown are the means \pm one and 1.96 Std. Dev. for five replicate samples at each site; p values are for post hoc tests (Tukey's HSD) following an ANOVA.

ganic matter were not significant between sites at the Bunker Hill location (Fig. 1a), but the Huntley virgin prairie (HV) had almost twice as much organic matter ($P < 0.01$, data from 1998) than the adjacent agricultural field (HA). In all sites except HA (no data available), the top 1 cm of soil contained significantly more organic matter ($P < 0.05$) than the soil sampled from between 5 and 7 cm.

Viable microbial biomass (phospholipid phosphate) was significantly different between sites at each location (BH and H; Figs. 1b, 2a) with the exception that the forest site (BHF) at Bunker Hill was not significantly different from the virgin prairie site (BHV; Fig. 3a). The differences in microbial biomass between the virgin (BHV) and restored (BHR) prairies at Bunker Hill were only significant in the top 1 cm of soil, but not at the 5–7 cm depth (Fig. 1b), possibly due to the greater tendency for the BHR soil to dry out at the surface (mean \pm SD % moisture for BHR = 6.3 ± 1.1 ; BHV = 19.3 ± 2.0). However, the differences in microbial biomass between the two Huntley sites were highly significant in both depths sampled (Fig. 2a), with the agricultural field containing very little viable biomass compared to any of the other sites sampled (Fig. 3a). Although virgin prairie soil sampled at the James Woodworth Prairie (JWV) site had significantly more organic matter than any of the other sites regardless of depth (Table 2), it had about the same amount of microbial

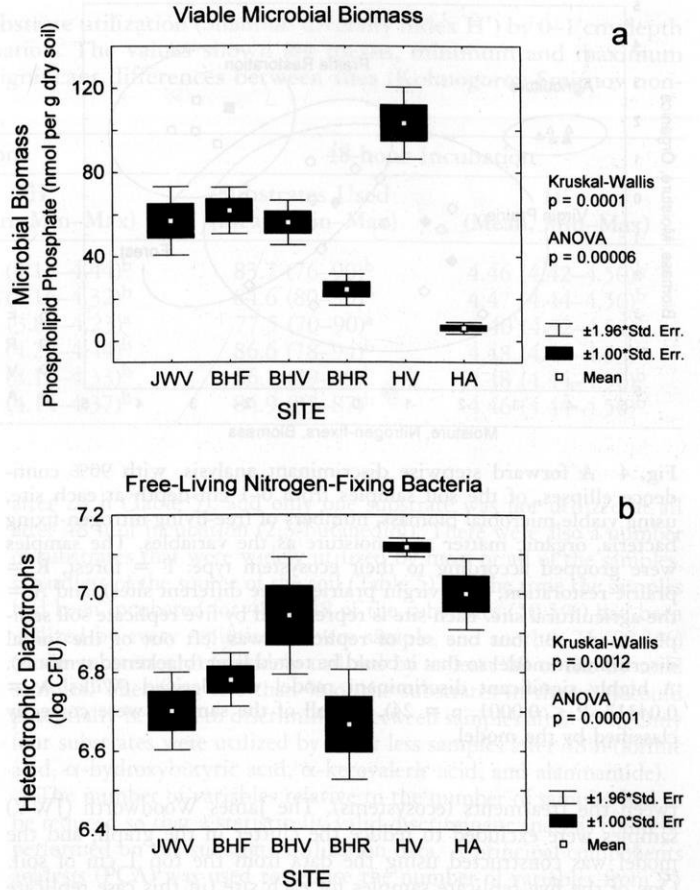


Fig. 3 Soil (a) viable microbial biomass and (b) numbers of free-living nitrogen-fixing bacteria in each of six sites sampled (see Tables 1 and 2 for site descriptions). Soil was sampled from a depth of 0–1 cm. Values shown are the means \pm one Std. Error and one Std. Dev. for five replicate samples at each site; p values are for an ANOVA and a non-parametric ANOVA (Kruskal-Wallis test).

biomass as BHV and less than HV (Fig. 3a). So, although viable microbial biomass was significantly positively correlated with % organic matter overall (Pearson's $r = 0.529$, $P < 0.01$, $n = 50$), there were some exceptions to this rule. These differences might also be attributable to moisture because the Huntley site was sampled after a heavy rain and was wetter at the surface than the other sites, whereas the Bunker Hill and James Woodworth soils had roughly equivalent moisture contents when sampled (Table 2).

At the Bunker Hill location, the same pattern held for nitrogen-fixers as for total microbial biomass (Figs. 1b, 1c). In contrast, although the agricultural field (HA) had significantly less total microbial biomass than the virgin prairie (HV), the counts of nitrogen-fixers were not significantly different (Figs. 2a, 2b) and were among the highest of any of the sites sampled (Fig. 3b). Subsequent soil analyses performed in 1998 did not find significant differences in nitrate concentrations between these soils. It may be that a lack of organic nitrogen in the HA soil was selecting for an enrichment of nitrogen fixers relative to total microbial biomass, although only total soil organic matter (not organic nitrogen) was measured in this study.

When the biomass, nitrogen-fixer, organic matter and moisture data were entered as variables into a forward stepwise discriminant analysis, the model (Fig. 4) was able to accurately discriminate be-

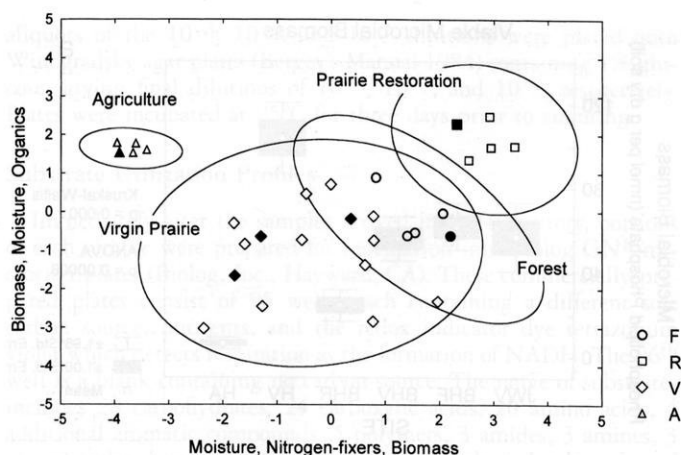


Fig. 4 A forward stepwise discriminant analysis, with 90% confidence ellipses, of the soil samples from 0–1 cm depth at each site, using viable microbial biomass, numbers of free-living nitrogen-fixing bacteria, organic matter and moisture as the variables. The samples were grouped according to their ecosystem type: F = forest, R = prairie restoration, V = virgin prairie (three different sites), and A = the agricultural site. Each site is represented by five replicate soil samples ($n = 30$), but one set of replicates was left out of the initial discriminant model so that it could be tested later (blackened symbols). A highly significant discriminant model was derived (Wilks' $\lambda = 0.04317$, $P < 0.0001$, $n = 24$), and all of the samples were correctly classified by the model.

tween the treatments (ecosystems). The James Woodworth (JWV) samples were excluded to reduce the clutter in the graph, and the model was constructed using the data from the top 1 cm of soil. One of the five replicate samples for each site (in this case replicate #3 for each site) was excluded to later test the model for classification accuracy. The Wilks' Lambda was highly significant ($\lambda = 0.04317$, $P < 0.0001$, $n = 24$), and only one of the 24 samples entered into the original model was misidentified (BHV5 was identified as a BHF forest sample), giving a total of 95.8% correct identifications. When the six excluded replicates were then added into the model to test its validity, they were classified with 100% accuracy. The significance of the results was not dependant upon which set of replicates was initially excluded.

Table 3. Substrates metabolized at significantly different rates after 24 hours of incubation in the Biolog assay by virgin prairie (BHV) soils and by prairie restoration (BHR) soils at the Bunker Hill site (0–1 cm depth). In each case, the BHV soil microbial communities metabolized the substrates at a significantly faster rate than did the BHR soil communities (P values are given below for a Kolmogorov-Smirnov two-sample nonparametric test). Substrates that were also metabolized faster by the Huntley virgin prairie (HV) communities than by the Huntley agricultural site (HA) communities are marked with **($P < 0.025$) or with *($P < 0.100$).

$P < 0.001$	$P < 0.005$	$P < 0.025$	$P < 0.100$
D, L-lactic acid	acetic acid	L-arabinose	γ -hydroxybutyric acid*
quininic acid	citric acid	tween 40	α -ketobutyric acid
L-histidine	D-saccharic acid	tween 80	succinic acid
hydroxy L-proline	sebacic acid	cis-aconitic acid	L-asparagine
L-serine*	p-hydroxyphenylacetic acid	α -ketoglutaric acid	putrescine
urocanic acid**	L-aspartic acid	D-galactonic acid lactone	
	γ -aminobutyric acid	succinamic acid**	
	inosine	L-pyroglutamic acid	
		thymidine	
		2-aminoethanol	

An examination of the 90% confidence ellipses for the data grouped by ecosystem (Fig. 4) showed that there was considerable overlap between the forest and virgin prairie sites but very little overlap between the prairie restoration and the virgin prairies. The agricultural site had no overlap with any of the other groups. Biomass, moisture and numbers of nitrogen fixers were most useful in separating the groups along Root 1 (the x-axis), while biomass, moisture and organics were most important in Root 2 (the y-axis). If the JWV samples were included in the model along with all of the replicates (including both depths), the Wilks' lambda was still highly significant ($\lambda = 0.14259$, $P < 0.0001$, $n = 60$), and the classification of samples was 83.3% correct.

Substrate Utilization Profiles

The Biolog GN substrate-utilization plates were incubated at 27°C (close to the average surface soil temperatures), and readings were taken at 24 and 48 h. Although some bacterial growth, death and populations shifts certainly occurred during sample preparation and incubation, little color development (measurable respiration) was observed in the wells during shorter incubations.

The pattern of sole carbon source utilization differed between sites more than within sites. For 24 of the 95 substrates tested, the virgin prairie soil at Bunker Hill (BHV) responded faster than the restoration soil (BHR) at the same location, and an additional five substrates were borderline significant after 24 h (Table 3). There were no substrates that were respired more quickly by BHR than by BHV. Only three substrates were respired more quickly by the Huntley virgin prairie (HV) soils than by the adjacent agricultural (HA) soil after 24 h (Table 3), and no substrate was utilized more quickly by HA than by HV.

After 24 hours of incubation, only 12 of the 95 substrates had been respired in a manner that correlated significantly with the microbial biomass of the soil sample. The utilization rates of cellobiose and D-trehalose correlated best with the organic content of the samples (Pearson's $r = 0.72$, $n = 25$), with D-gluconic acid close behind ($r = 0.70$); respiration of 17 other substrates also correlated significantly with organic content. None of the substrates' utilization rates correlated negatively with biomass or organic matter, but the use of four substrates correlated negatively with the number of nitrogen fixers (xylytol, D-mannose, gentibiose and D-trehalose). Nine other substrates correlated positively with the number of nitrogen-fixers.

The total number of substrates utilized by each sample was tallied

Table 4. Number of Biolog substrates utilized and diversity of substrate utilization (Shannon diversity index H') by 0–1 cm depth soil samples from various sites after 24 and 48 hours of incubation. The values shown are means, minimum and maximum values ($n = 10$; for JWV $n = 15$). Superscript letters indicate significant differences between sites (Kolmogorov-Smirnov non-parametric test. $P < 0.05$).

Site	Ecotype	24-hour Incubation		48-hour Incubation	
		Substrates Used (Mean, Min–Max)	H' (Mean, Min–Max)	Substrates Used (Mean, Min–Max)	H' (Mean, Min–Max)
JWV	Virgin prairie	59.4 (50–71) ^c	4.26 (4.14–4.44) ^b	83.7 (76–90) ^b	4.46 (4.42–4.50) ^b
BHV	Virgin prairie	52.9 (47–59) ^c	4.24 (4.16–4.32) ^b	84.6 (80–90) ^b	4.47 (4.44–4.50) ^b
BHR	Restoration	26.6 (11–43) ^a	4.07 (3.80–4.23) ^a	77.5 (70–90) ^a	4.40 (4.32–4.51) ^a
BHF	Forest	50.9 (43–56) ^c	4.28 (4.20–4.44) ^b	86.6 (78–94) ^b	4.48 (4.41–4.53) ^b
HV	Virgin prairie	39.3 (21–50) ^b	4.25 (4.16–4.33) ^b	86.1 (79–89) ^b	4.48 (4.44–4.50) ^b
HA	Agriculture	37.4 (27–47) ^{ab}	4.21 (4.14–4.37) ^b	84.9 (83–87) ^b	4.46 (4.44–4.50) ^b

to get a sense of the “richness” of substrates used by the various soils (Table 4). In order to be scored as positive, a microtiter plate well had to have a relative density reading of greater than 1 on the 0–4 scale. After 24 h of incubation, two of the virgin prairies (JWV and BHV) and the forest (BHF) had utilized the most different substrates (Table 4). The prairie restoration site (BHR) had the lowest number of substrates utilized, less than half that used by JWV. The Huntley agriculture site (HA) was not significantly different from the BHR site in terms of number of substrates used, but surprisingly the Huntley virgin prairie site (HV) was significantly lower than the other virgin prairies and was not significantly different from HA. After 48 h, many of the differences in richness of substrate utilization had disappeared, as each of the samples had utilized nearly all of the substrates by this time, but BHR had still used significantly fewer substrates than any other site.

In order to get a sense of the relative “diversity” of substrates utilized, a modified Shannon Diversity Index, H' , was also calculated for each sample (Table 4). The diversity indices showed fewer differences between sites than richness, with only BHR being significantly ($P < 0.05$) lower than all of the other samples at both 24 and 48 h incubation periods (Table 4).

There were also some differences in which substrates were utilized (reading > 1 on the relative scale) by various samples according to ecosystem or location. The two Cook County virgin prairies, JWV and BHV, had several substrates in common which were not used as frequently by any of the other samples after 24 h: Tween 40, Tween 80, mono-methylsuccinate, acetic acid, propionic acid, sebacic acid, L-proline, thymidine and D-galactonic acid lactone (which was also used by BHF). Each of these sites had only one substrate unique to that site and not used by any other sites after 24 h (D-arabitol for JWV, and succinamic acid for BHV), indicating that these two sites had more metabolic potentials in common than they had differences. Sites JWV and HV (virgin prairies from different counties) had only two substrates in common after 24 h that were not used by the other samples: γ -hydroxybutyric acid and 2-amino ethanol. Also emphasizing the importance of location, there were several substrates that were utilized less frequently or not at all by the two McHenry County sites (HV and HA) but were used by soils from the other sites after 24 h (D-galactose, gentibiose, D-raffinose, L-rhamnose, glycerol, D,L- α -glycerol phosphate and glycogen) or not used at all after 48 h (acetic acid and formic acid). Only one substrate was utilized at a greater frequency by both the HV and HA sites than by the other sites (α -cyclodextrin was used by every Huntley replicate within 48 h).

As might be expected from rich, mixed-species communities, there were only nine substrates not utilized by any of the samples

after 24 h (Table 5), and only one substrate was not utilized at all after 48 h of incubation (2,3-butanediol). There were also a number of substrates that were widely utilized by most or all of the samples, regardless of the source of the soil (Table 5). By the time the samples had been incubated for 48 h, 48 of the substrates (50.5%) had been utilized by every replicate of every sample, and another 21 (22.1%) of the substrates were widely utilized by at least 60 of the 65 total samples. Therefore, less than $\frac{1}{3}$ of the substrates in the assay could potentially be used to discriminate between samples after 48 h. Only four substrates were utilized by 15 or less samples after 48 h (formic acid, α -hydroxybutyric acid, α -ketovaleric acid, and alaninamide).

The number of variables relative to the number of samples had to be reduced so that a statistically valid discriminant analysis could be performed on the substrate utilization data. A principal components analysis (PCA) was used to reduce the number of variables from 95 to 20 by selecting those substrates that best explained the differences between the samples in terms of the constructed factors (axes). Only the Bunker Hill samples were used in the PCA so as not to bias the discriminant analysis results. Only those substrates with significant factor loadings on the first two factors (axes) of the PCA were included in the discriminant analysis.

Of the 20 substrates entered into the forward stepwise discriminant analysis of the samples from the 24 h incubation of the soil from the top 1 cm depth, 13 were included in the discriminant model (Table 6). Nine of these substrates were ones that had shown significant differences between treatments (Table 3). The other four substrates included in the model either exhibited significance only in a multi-way comparison (D-mannitol and D,L- α -glycerol phosphate) or were metabolized significantly faster by the forest sample (BHF) than by all of the other sites (D-galactose and D-melibiose).

Replicate #3 from each site was initially excluded from the discriminant model for later testing. The discrimination was significant (Wilks' lambda = 0.02568, $P < 0.0001$, $n = 52$), and only one sample was misclassified (BHF 4b was classified as virgin prairie; Fig. 5). The factor structure included quinic acid, inosine, urocanic acid, D-saccharic acid, L-serine and hydroxy L-proline on Root 1 and D-galactose, quinic acid, cis-aconitic acid, D,L- α -glycerol-phosphate, D-melibiose and γ -hydroxybutyrate on Root 2. When the 13 replicates initially omitted were added as a test of the discriminant model, only two were misclassified (BHF 3b was classified as virgin prairie, and JWV 3c was classified as forest), giving an overall accuracy of 84.6%.

Samples from the 5–7 cm depth that were incubated for 24 h also provided a significant discrimination between treatments. Samples incubated for 48 h did not provide a clear separation between treatments, and the discrimination was not significant.

Table 5. After 24 hours of incubation, substrates not utilized by any soil sample replicates, substrates rarely utilized (no more than 3 positive samples), or widely utilized (at least 50 positive samples), regardless of the site sampled. For the six sites sampled (BHF, BHR, BHV, HV, HA, JWV), 10 replicate Biolog plates were incubated for each site (except JWV, which had 15 replicate plates); total n = 65. For these substrates, there were no significant between-site differences.

Not Utilized	Rarely Utilized	Widely Utilized
i-erythritol	α -cyclodextrin	N-acetyl-D-glucosamine
α -D-lactose lactulose	adonitol	D-fructose
xylitol	L-fucose	α -D-glucose
α -hydroxybutyric acid	formic acid	D-mannitol
glycyl-L-aspartic acid	D-glucosaminic acid	D-mannose
glycyl-L-glutamic acid	α -ketobutyric acid	β -methyl-D-glucoside
L-leucine	α -ketovaleric acid	D-sorbitol
L-threonine	alaninamide	sucrose
2,3-butanediol	L-ornithine	D-trehalose
	L-phenylalanine	D-galacturonic acid
	D, L-carnitine	D-gluconic acid
		D-glucuronic acid
		D, L-lactic acid
		glucose-1-phosphate
		glucose-6-phosphate

Table 6. Biolog substrates included in the discriminant analysis of the 24-hour incubation of soils sampled from the top 1 cm. A principal components analysis (PCA) was used to determine which substrates explained the most variance between samples. These 20 substrates were then entered into a stepwise discriminant analysis, which resulted in the inclusion of the 13 substrates listed below in the discriminant model.

Carboxylic Acids	Carbohydrates	Amino Acids	Aromatics	Phosphorylated Compound
quinic acid	D-galactose	L-serine	urocanic acid	D, L- α -glycerol phosphate
cis-aconitic acid	D-mannitol	hydroxy L-proline	inosine	
γ -hydroxybutyric acid	D-melibiose			
succinamic acid				
D-saccharic acid				

In a further test to determine whether the discrimination in the 24 h samples was specific to the ecosystem treatment, discriminant analyses were also performed using soil sample replicate number or Biolog plate replicate number as the grouping variables. As would be expected if the discrimination of the sites depended upon ecosystem treatment and was not random, the discriminant models using replicate number or plate number were not significant and could not correctly classify samples by these categories. When site location (Bunker Hill, James Woodworth or Huntley) was used as the grouping variable, the program could separate the samples by location, indicating that some of the differences between samples could be accounted for by landscape heterogeneity rather than management treatment.

DISCUSSION

It is clear from these results that both the ecosystem (or ecosystem management) and the location of the sites had significant effects on the soil microbial communities. Total viable microbial biomass appeared to be limited primarily by soil moisture and organic matter, both of which were related and declined as a result of soil disturbance in this study (sites BHR and HA, Table 2 and Fig. 3a). Bacteria, in particular, depend upon films of water in soil for their activity (substrate uptake and metabolism) and motility (Gregorich and Janzen 2000, Rice et al. 1998). Soil organic matter increases the water-holding capacity of the soil (Baldock and Nelson 2000), among other

characteristics favorable to microbes (increased cation exchange capacity, buffering capacity, and sources of slow-release nutrients).

The biomass of the agricultural site (HA) may also have been depressed somewhat due to increased acidity (mean pH 5.9) because most soil bacteria have pH optima between 6.0 and 7.5 (Gregorich and Janzen 2000). Fungi easily withstand lower pH values, but they often decline in tilled soils due to physical disruption of their hyphae (Wardle 1995) or lack of moisture (Frey et al. 1999). Similar reductions in the overall microbial biomass of grassland soils due to agricultural activities have been reported in many countries (Patra et al. 1990, Zelles et al. 1995, Lavahun et al. 1996, Alvarez et al. 1998).

The variability in microbial biomass within sites was greatest in the undisturbed virgin prairie and forest soils. As would be expected, the more recently a site had been disturbed (plowed), the more uniform the distribution of microbial biomass was with both depth and area (Figs. 1b, 2a, 3a). Similar depth results have been found by others (Lavahun et al. 1996, Alvarez et al. 1998). Our results also agreed with those of others who have found that microbial C and N in tallgrass prairie soils are concentrated at the surface (Garcia and Rice 1994) where the concentration of organic matter is also highest (Ransom et al. 1998).

In general, the viable biomass results agreed with those previously obtained by direct counting of live bacterial cells in a tallgrass prairie soil in Missouri (Herman and Kucera 1976). Those authors found

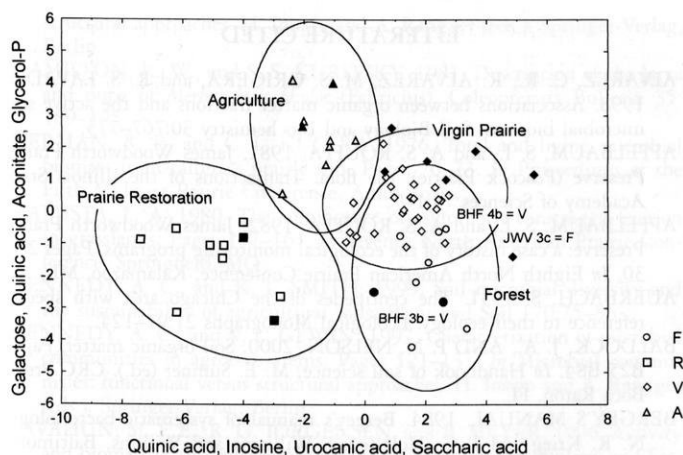


Fig. 5 A discriminant analysis, with 90% confidence ellipses, of the soil samples from 0 to 1 cm depth incubated in the Biolog assay for 24 hours. Twenty substrates chosen by PCA were entered into the forward stepwise analysis, which used 13 of those substrates in the discriminant model (Table 6). The samples were grouped according to their ecosystem type: F = forest, R = prairie restoration, V = virgin prairie (three different sites), and A = agricultural site. Each site is represented by five replicate soil samples, and two replicate Biolog plates were inoculated for each sample (except for JWV, which had three replicate plates; total $n = 65$). One set of replicates for each site was left out of the initial discriminant model for later testing (blackened symbols), and a highly significant model was derived (Wilks' $\lambda = 0.02568$, $P < 0.0001$, $n = 52$). In the initial construction of the model, one sample was misclassified (BHF replicate 4b); when the replicates initially omitted were later entered into the model, two were misclassified (JWV 3c and BHF 3b), giving an overall accuracy of discrimination of 84.6%.

1.6×10^8 live bacterial cells/g dry soil in a control area and 2.3×10^8 cells/g in an annually burned area. The virgin prairies sampled in the present study ranged from 3.8×10^8 to 1.2×10^9 live cells/g dry soil, if one uses a conversion factor of 1×10^7 cells per nmol phosphate from lipids as a rough estimate of cell numbers, or 7.6×10^{10} to 2.4×10^{11} if a conversion factor of 2×10^9 cells per nmol P is used (Dobbs and Findlay 1993). In contrast, the agricultural site had more than an order of magnitude fewer cells/g of soil. One might expect higher estimates of biomass from the phospholipid phosphate assay than from direct counting, because the lipid assay will include bacteria obscured by debris as well as live fungi, protozoa, algae and possibly microinvertebrates.

Surprisingly, in the agricultural site (HA) the asymbiotic nitrogen-fixing bacteria were significantly enriched relative to the total microbial biomass (Figs. 2b, 3b). Possible explanations include natural selection based upon nitrogen limitations at periods between fertilizer applications, possibly as a result of lower levels of stable soil organic nitrogen and a reduced ability to hold nutrients via cation exchange and adsorption due to the relative lack of organic matter in this soil (Baldock and Nelson 2000). One would think, however, that the lack of soil organics would also restrict the growth of heterotrophic diazotrophs, because it has been proposed that these organisms are most limited by the availability of a suitable carbon source (Kapusta 1980). It is possible that the presence of a legume crop (soybeans) in the field at the time of sampling may have increased the numbers of nitrogen fixing bacteria in the soil, because *Rhizobium* can survive saprophytically in the soil for extended periods (Graham 2000). However, a wide variety of colony morphologies were observed on the plates containing nitrogen-free media, suggesting that increased numbers of *Rhizobium* alone were unlikely to

account for the increase in nitrogen fixers seen at this site. The presence of colonies on these plates does not reflect actual nitrogen-fixation activity in the soils, and we have no way of telling from these data whether or not the organisms were active *in situ*. Nitrogen-fixing bacteria generally perform best when nitrogen is limiting, the pH is near neutral (Brady 1974), and clays are present to protect them from oxygen and predators (Pankhurst 1997).

Substrate utilization profiles like those provided by the Biolog assay have been proposed as useful indicators of functional phenotypic diversity in microbial communities (Garland and Mills 1991, Griffiths et al. 1997, Palojarvi et al. 1997). In the current study, clear differences were seen between sites in the short-term (24 h) metabolic responses of the microbial communities to certain substrates (Tables 3, 4, Fig. 5). However, by the time the samples had been incubated for 48 h, most of them were metabolizing nearly all of the substrates, and we were unable to discriminate between sites based upon substrate utilization patterns.

At least half of the substrates utilized within 24 h by nearly all of the samples (≥ 50 out of 65 samples) were carbohydrates, particularly simple sugars, sugar phosphates, or disaccharides commonly found in plant litter or plant root exudates (Table 5). However, the substrates that were metabolized at significantly different rates within 24 h by virgin prairies (BHV, HV) compared with disturbed sites (BHR, HA) included (Table 3) 13 carboxylic acids, six polar amino acids, four aromatics, and an unusual sugar (L-arabinose), indicating that the differences between treatments may rest largely in the ability to respond quickly to a wider variety of molecular arrangements. The rapid response of the virgin prairie soils in particular in terms of the number of substrates utilized (Table 4) was not surprising, because microbial activity in prairies is often found to be much higher than in soils from other native ecosystems in the same climate (Rice et al. 1998). It may be that the wealth and diversity of organic matter and plant exudates in prairie soils stimulates the development of a population of microbes capable of utilizing a wide range of substrates. The long-term stability of these systems may allow them to develop species-rich "climax" microbial communities exhibiting the highest possible diversity and biomass under the given environmental conditions (Fliebbach and Mäder 1997), while the constant disturbance of cultivated sites may leave them in a constant state of early succession with lower species diversity.

It was somewhat surprising, however, that the agricultural soil (HA) exhibited slightly greater richness and diversity of substrate utilization than the site that had been under prairie restoration management for 12 years (BHR; Table 4), even though BHR had significantly more viable microbial biomass (Fig. 3a) and organic matter. The difference in initial substrate utilization rates may have been due in part to the lower soil moisture levels of the BHR site on the day that it was sampled, possibly leading to increased cell dormancy and lag times for the bacteria.

No other studies reported thus far have evaluated tallgrass prairie soils using the Biolog system. In a comparison of farming practices in Switzerland, the organically farmed soils had higher microbial biomass and utilized more carbohydrate substrates than the conventional and NPK-fertilized soils, but there were no significant differences in the use of the other Biolog substrates (Fliebbach and Mäder 1997). Unlike the present study, these investigators did not find correlations between the microbial parameters and the organic carbon or organic nitrogen content of the soils (Fliebbach and Mäder 1997). Another European study found that the Biolog assay could discriminate between agricultural soils from different countries that had been under different management practices for many years but could not discriminate between different short-term treatments like mulching or straw addition (Palojarvi et al. 1997), echoing our findings of

long-term, landscape-level differences in substrate utilization patterns.

Although they did not use the Biolog assay, Kennedy and Smith (1995) compared substrate utilization rates of pure cultures isolated from "natural prairie" and cultivated sites near Pullman in eastern Washington. They found that the prairie soil had greater microbial biomass carbon and enzyme activity rates for phosphatase, dehydrogenase, denitrification and nitrification but that both ecosystems utilized about the same range of substrates tested. However, they found that the cultivated soil microbes were often more resilient in their response to stressors such as heavy metals, antibiotics and osmotic pressure. Our results may differ because they reported fungi to be dominating the decomposition activity at the prairie site (Kennedy and Gewin 1997), while our inoculation and assay methods favored the growth and detection of bacteria.

Inoculation of Biolog plates with diluted soil suspensions always carries with it the possibility that some carbon sources and nutrients may be carried over from the soil to the inoculated wells (White et al. 1997), confounding the carbon substrate utilization results. However, because the HA sample had the lowest soil organic content and yet responded more quickly to certain substrates than BHR and almost as quickly as HV (Table 4), we doubt that this was a significant problem in this study. The Biolog assay conditions also typically stimulate the growth of bacteria within the microtiter plate wells whether or not the organisms utilize the carbon source being tested. This opens up the possibility of microbial selection and competition occurring within the wells over time (Winding and Hendriksen 1997), which is why we chose to use the shortest incubation times possible in this study. However, the microbial communities in the wells cannot be assumed to be identical to those *in situ*, considering the possible effects of sample processing and incubation. It is possible that the mixing, dilution and settling techniques used to equalize the OD of the soil solutions may have been biased toward certain cell shapes (cocci vs. bacilli, for example) or certain cell sizes (starved microcells vs. viable cells).

Overall, these results reinforce the notion that there are negative, long-term effects of conventional agriculture on soil and microbial community health. With the loss of soil organic matter, microbial biomass and some microbial functions, these highly disturbed soils may have lost a good deal of their overall function and resilience. Even though the agricultural site (HA) was sampled at a time that soil moisture should not have been limiting (after a recent rain), it still had significantly less viable microbial biomass than the somewhat dryer prairie restoration site (BHR). Further studies need to be done to examine seasonal trends and spatial variability in greater detail as well as to better determine the physical and chemical factors structuring the microbial communities in these soil ecosystems. It appears that prairie restoration projects may improve the microbial biomass, and ultimately the soil organic matter, of disturbed sites, but it may take many years or decades for these sites to reach the microbial biomass, activity and functional diversity levels found in virgin prairies.

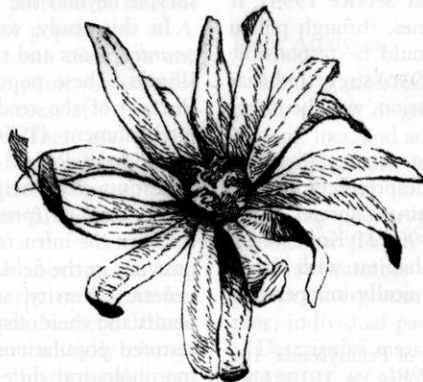
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Characterizing Three Restored *Andropogon gerardii* Vitman (Big Bluestem) Populations Established with Illinois and Non-Illinois Seed: Established Plants and Their Offspring

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Patterns of isozyme variation and morphological traits of *Andropogon gerardii* (big bluestem) were studied in three restored tallgrass prairies in Illinois. These three populations differed in seed source (non-Illinois and Illinois), time since establishment (1970s and 1990s), and spatial distribution within the Goose Lake Prairie State Natural Area, Grundy County, Illinois. Analysis of established plants in the field showed the non-Illinois *A. gerardii* to be genetically and morphologically different to the *A. gerardii* from Illinois. These restored non-Illinois populations maintained their genetic identity for more than 20 years, despite evidence from isozyme analysis of the offspring indicating gene flow between the non-Illinois and Illinois populations. If seedling recruitment were rare in established *A. gerardii* populations, then introgression of non-local genes into the local populations would likely take many generations, depending on the fitness of intraspecific hybrids relative to the native genotypes. Genetic diversity increased with the age of the restored population, while there was no appreciable difference in outcrossing rates. An interesting result of this study was that seed collected from the local Illinois plants did not ensure that the genetic composition of the seed was exclusively Illinois. This result is significant because it shows that gene flow between Illinois and non-Illinois populations can alter the genetic composition of the seeds from a presumably local source. Documentation of the location of the seed source populations used in restoration projects is essential if we are to stop the accidental introduction of non-local (and cultivar) genes into local restoration projects.

INDEX DESCRIPTORS: isozyme diversity, local and non-local seed, conservation genetics, tallgrass prairie.

Prairie restorationists throughout the United States have made great strides in restoring the species composition and structural components of the tallgrass prairie. Unfortunately, little is known about the genetic composition of these restored prairies. Gene flow among genetically divergent restored populations has become a major concern in the restoration of plant populations because of the potentially disruptive effects upon locally adapted genotypes (Montalvo et al. 1997). A baseline genetic study of *Andropogon gerardii* Vitman (big bluestem) from remnant and restored prairies in Illinois and three commonly used cultivars showed that these restored populations were more genetically similar to the cultivars than were the remnant Illinois populations (Gustafson 2000). This result was surprising given the strong emphasis placed on using 'local' seed and avoiding the intentional introduction of non-local or cultivar seed directly into restoration projects (Schramm 1990, U. S. Forest Service 1994). It was speculated that introgression of cultivar genes, through pollen dispersal, into the native Illinois populations could be responsible for these associations. Rhymer and Simberloff (1996) suggested that such introgression, rather than inbreeding depression, was the larger threat compromising natural ecosystems.

Andropogon gerardii Vitman (big bluestem) is a native, polyploid, warm-season, perennial prairie grass that is a widespread component of the North American prairie biome and a dominant species of the tallgrass prairie (Risser et al. 1981, Keeler 1990, McKone et al. 1998). This species has a rhizomatous growth habit with short-lived physical interconnections, resulting in physically independent

ramets of the same genet (Hartnett 1989). *Andropogon gerardii* is a complex polyploid with two polyploid cytotype races (hexaploid $2n = 6x = 60$ and enneaploid $2n = 9x = 90$), with an increased frequency of the enneaploids in the western range of the species (Keeler 1990). The $9x$ cytotypes were typically taller and produced more biomass than the $6x$ cytotypes, with no difference in seed produced per unit area (Keeler and Davis 1999). These polyploid cytotypes interbreed and produce fertile euploids and aneuploids, although aneuploids are rarely observed in nature (Keeler 1992, Norrmann et al. 1997). *Andropogon gerardii* has a pre-zygotic incompatibility mechanism (failure of the pollen tube to penetrate and grow into the style) that results in low seed set (0.2–6.0%) following self-pollination (Norrmann et al. 1997). In addition, post-zygotic mechanisms are also apparently present, as self-pollinated offspring do not survive beyond the first growing season (Norrmann et al. 1997).

In this study, we examined isozyme variation in established *A. gerardii* plants and their offspring from three restored populations in Illinois. These populations differed in the origin (non-Illinois and Illinois) of the seed used to establish the populations, time since establishment (1970s or 1990s), and spatial distribution within Goose Lake Prairie State Natural Area, Illinois. We also measured maximum plant height, number of culms, number of infructescences, insect damage (presence/absence) and maturity (presence of green tissue in the infructescence) of the Illinois and non-Illinois *A. gerardii* growing in the field. The objectives of this study were to: 1) estimate genetic diversity and relationship among established *A. gerardii* plants and their offspring; 2) test for genetic structuring within these restored populations; 3) estimate outcrossing rates; and 4) test for morphological differences between non-Illinois and Illinois *A. gerardii* growing in the field.

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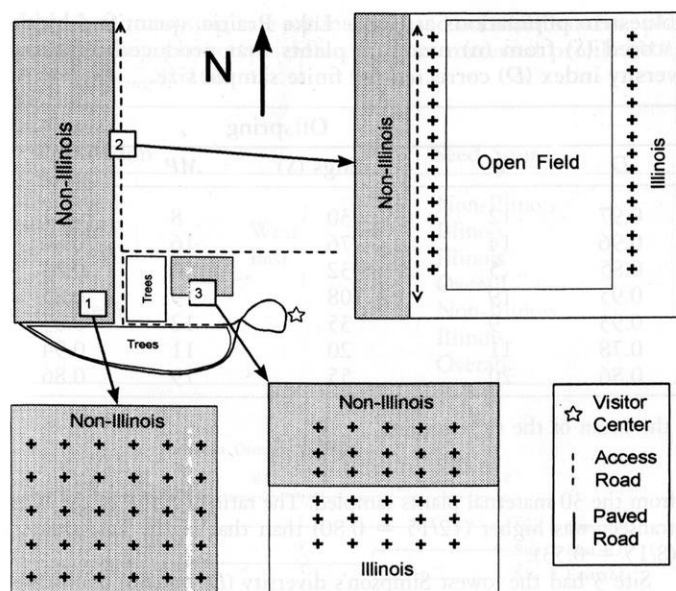


Fig. 1. Site map (not to scale) with the location and sampling strategies illustrated for the three restored *Andropogon gerardii* populations sampled at Goose Lake Prairie State Natural Area, Illinois. (+) Indicates the location of individual collections.

METHODS

Study Sites and Plant Material

Goose Lake Prairie State Natural Area (hereafter referred to as Goose Lake Prairie), Grundy County, Illinois, is located approximately 80 km southwest of Chicago and 1.5 km southwest of the confluence of the Kankakee and Des Plaines Rivers. The original 97 ha site was purchased by the State of Illinois in 1969. With subsequent additions of land in the 1970s, Goose Lake Prairie now totals 1027 ha of remnant and restored tallgrass prairie (site manager pers. comm.).

Vegetative material from flowering plants was collected on 25 July 1998, in the three sites that were selected for this study (Fig. 1). The first location (Site 1) was a 17 ha prairie restored in 1976 with Wilson seed from Nebraska (site manager, pers. comm.). The original source for the Wilson seed could not be determined from the bill of sale; however, the source is likely one of two cultivars ('Kaw' from Kansas or 'Pawnee' from Nebraska) developed and released from the Plant Material Center in Manhattan, Kansas. Whether a Kansas or Nebraska cultivar, the Wilson seed was considered a non-Illinois seed source. Site 1 was used to investigate fine-scale patterns of isozyme variation in a single-seed source (homogeneous) population of *A. gerardii*. Six transects were located in a north-south direction and spaced five m apart. A single flowering *A. gerardii* plant was sampled approximately every five m along each transect (total of five plants per transect) using a random stratified procedure. These plants were marked with survey flags, and fresh leaf material was collected from each plant. For all sites, fresh leaf material was stored on ice, transported to Southern Illinois University Carbondale (SIUC), extracted, and stored at -80°C .

The second location (Site 2) was a large prairie abutting the non-Illinois *A. gerardii* (Site 1) that was restored in the middle to late 1980s with local seed from Mason County State Nursery, Illinois (site manager, pers. comm.). This entire area was initially planted using a seed drill, which was evident by the regular spatial distribution (1 m intervals) of the established plants. A 150 by 200 m

section (hereafter referred to as the 'Open Field') did not become established with prairie plants and contained no flowering *A. gerardii* plants during our study. Site 2 was used to investigate patterns of isozyme variation in Illinois *A. gerardii* planted adjacent to and 150 m from the non-Illinois population. Two transects were established in a north-south orientation, with the west transect located in the Illinois *A. gerardii* population juxtaposed to the non-Illinois population and the east transect located 150 m to the east across the open field (Fig. 1). A total of 15 flowering *A. gerardii* plants were sampled (random stratified) at approximately 10 m intervals, marked with survey flags, and fresh leaf material was collected.

The third location (Site 3) was established in 1994 and consisted of two discreet subpopulations. The northern half was planted with seed from Site 1 (originally Wilson seed, non-Illinois). The southern half of the site was planted with Illinois *A. gerardii* (Mason County State Nursery, Illinois) (Fig. 1). Casual observation revealed differences in plant size with the non-Illinois plants smaller than the Illinois plants. This site was used to investigate patterns of isozyme variation in a prairie restored with distinct non-Illinois and Illinois *A. gerardii* subpopulations. Five parallel transects (five m apart) were established perpendicular to the east-west demarcation line separating the two populations. Six plants (three of non-Illinois and three of Illinois origin) were sampled per transect using a randomly stratified sampling procedure, marked with survey flags, and fresh leaf material was collected.

On 27 September 1998, maximum height, number of flowering culms, number of infructescences, presence/absence of insect damage and green tissue in the infructescence were recorded on marked plants in Site 1 and Site 3. Seeds were collected from the 30 marked plants in each of the three sites, transported to SIUC, and stored at 4°C . In March 1999, the seeds were germinated, grown in petri dishes for seven days, and then extracted for the isozyme analysis.

Isozyme Electrophoresis

Approximately 0.5 g of fresh leaf material (maternal plants or seedlings) was homogenized in the Tris-HCl extraction buffer of Wendel and Weeden (1989), centrifuged at 10,000 r.p.m. (12,000 g) for 15 min and the supernatant stored frozen (-80°C) in 1.5 ml microcentrifuge tubes until needed. Enzyme separation was accomplished using 13% w/v starch gel (Starch Art hydrolyzed potato starch, Smithville, TX). Four enzyme systems, coding for five putative loci, were assayed using a Tris EDTA Borate pH 8.0 gel/electrode buffer system. Enzyme staining protocols followed Wendel and Weeden (1989). The following enzyme systems (with locus abbreviations and enzyme commission numbers in parentheses) were used: aspartate amino transferase (AAT-2, 2.6.1.1), glucose phosphate isomerase (GPI-2, 5.3.1.9), malate dehydrogenase (MDH-1, 1.1.1.37) and phosphoglucosmutase (PGM-2, PGM-3, 2.7.5.1).

Data Analyses

Identification of alleles and assignment to specific loci was not possible with *A. gerardii*. Multiple polyploidy level (6x to 9x), overlapping loci, and additional gene duplication all appeared to interact and make genetic interpretation difficult. Therefore, for each enzyme system studied, individual band presence or absence and overall multibanding phenotypes were determined for each individual in each population (Dolan 1994) instead of standard measures of genetic variation (number of alleles, percent polymorphic loci) that require genetic interpretation. Although banding patterns were often complex, individual patterns were consistently obtained.

Descriptive measures of genetic diversity were calculated following Jonsson et al. (1996): (i) the number of ramets of maternal plants (R) or offspring seedlings (S) sampled; (ii) number of multilocus

Table 1. Maternal and offspring (seedling) diversity in three big bluestem populations at Goose Lake Prairie, quantified by the number of sampled maternal ramets (*R*), number of seedlings scored (*S*) from (*n*) maternal plants that produced offspring, distinguishable multibanding phenotypes (*MP*), and Simpson's diversity index (*D*) corrected for finite sample size.

Population	Seed Source	Maternal			<i>n</i>	Offspring		
		<i>R</i>	<i>MP</i>	<i>D</i>		Seedlings (<i>S</i>)	<i>MP</i>	<i>D</i>
Site 1	Non-Illinois	29	21	0.97	12	30	8	0.71
Site 2	West	15	12	0.96	14	76	16	0.80
	East	15	8	0.85	5	32	10	0.84
	Overall*	30	18	0.95	19	108	19	0.85
Site 3	Non-Illinois	15	10	0.93	9	35	12	0.83
	Illinois	15	7	0.78	11	20	11	0.94
	Overall*	30	15	0.86	20	55	19	0.86

*Overall *MP* and *D* values were calculated from the original data, not the mean of the sub-samples

phenotypes (*MP*); and (iii) Simpson's diversity index (*D*) corrected for finite sample size. To test for genetic structure, Jaccard's similarity and geographic distance between individual maternal plants within a population were compared using Mantel's test in the software package PC-ORD (McCune 1995). This procedure used a Monte Carlo randomization test (1000 iterations) which calculates the standardized Mantel's statistic (*Z*) of the observed data and the probability of exceeding this value by random chance. The null hypothesis was that genetic similarity between individual plants and geographic distances between them were not related.

Outcrossing rates could not be estimated using traditional diploid and tetraploid procedures, therefore outcrossing rates were calculated as: $OR = (\text{outcrossed offspring} / \text{total offspring}) * 100$. The maternal profile is the multilocus isozyme profile of the maternal plant in the field, while the multilocus isozyme profile of the seedlings produced from that maternal plant constitute the offspring profiles. All offspring that possessed different multibanding phenotypes than the maternal profile were the result of an outcrossing event. If the offspring multibanding phenotype had the same presence/absence profile as the maternal, they were considered to be the product of a selfing event. This descriptive approach overestimates the selfed progeny because it does not consider dosage effects. Offspring (AAAABB) with the same banding pattern as the maternal plant may not necessarily be the same genotype as the maternal plant (AABBBB), with both being coded as phenotype AB.

Population level relationships were investigated using Euclidean distance, based on frequency data, and cluster analysis (unweighted pair group method with arithmetic means—UPGMA) (McCune 1995).

Kruskal-Wallis tests were used to test for differences in maximum height, number of culms, number of infructescences, insect damage, and maturity measures of *A. gerardii* plants originally from the non-Illinois and local seed sources (SigmaStat 1995).

RESULTS

Diversity of Established (Maternal) Plants

Simpson's diversity estimates of the established *A. gerardii* populations ranged from $D = 0.85$ – 0.97 , with Site 1 (non-Illinois) the most diverse (Table 1). Site 1 had 21 distinguishable multilocus phenotypes (*MP*) identified from 29 plants sampled. Established in 1976, Site 1 was the oldest restored population included in this study.

The overall Simpson's diversity estimate for Site 2 ($D = 0.95$) was similar to Site 1 ($D = 0.97$), despite the 11% difference between the West and East transects (Table 1). There were 18 *MP* identified

from the 30 maternal plants sampled. The ratio of *MP/R* of the West transect was higher ($12/15 = 0.80$) than that of the East transect ($8/15 = 0.53$).

Site 3 had the lowest Simpson's diversity ($D = 0.86$) of all three sites and the largest difference (16%) between the two subpopulations (Table 1). The sampling scheme (spacing of sampling points and total area covered) and the method of establishing the prairie (via broadcasting seed) were similar to that of Sites 1, yet Site 3 Simpson's diversity estimate was 11% less than Site 1. The diversity estimates for the non-Illinois subpopulation (0.93) were similar to that of Site 1 (0.97) as well as the ratio of *MP/R*, 0.67 and 0.72 respectively. The local subpopulation diversity (0.78) and ratio of *MP/R* (0.47) were primarily responsible for lowering the overall diversity (0.86) of site 3.

Diversity of Offspring

Simpson's diversity was calculated from the offspring's isozyme profiles and corrected for the finite offspring sample size. This estimator does not correct for the sampling bias introduced by the limited number of maternal plants that produced offspring nor the autocorrelation among the offspring from the same maternal plant.

Sampling of the Site 1 offspring was restricted to less than or equal to three seedlings per maternal plant. The offspring genetic diversity (0.71) was 27% lower than the maternal (0.97) estimate (Table 1). This reduction could be the result of only 12 of the original 29 maternal plants producing offspring (41%). However, the ratio of *MP*/number of maternal plants with offspring ($8/12 = 0.67$) was similar to the *MP/R* ratio of the maternal population ($21/29 = 0.72$).

All of the offspring produced by the maternal plants from Site 2 and Site 3 were analyzed. Site 2 had a 10% decrease in genetic diversity between the maternal (0.95) and offspring (0.85) samples (Table 1). Approximately 63% of the maternal plants produced offspring, with 14/15 from the West transect and 5/15 from the East transect. Diversity estimates of the offspring from the two transects decreased by 16% (West) and 1% (East). Sixteen *MP* were identified from 14 maternal plants from the West transect (14% increase) while 10 *MP* from five maternal plants were identified in the East transect (100% increase).

There was no change in the overall Simpson's diversity between the maternal and offspring from Site 3, largely due to the non-Illinois subpopulation diversity decreasing by 10% while the Illinois subpopulation diversity increased by 16% (Table 1). Approximately 67% of the maternal plants produced offspring with 9/15 from the non-Illinois subpopulation and 11/15 from the local subpopulation.

Table 2. Outcrossing rate estimates based on multibanding phenotypes. Maternal multibanding phenotype ($MP_{maternal}$), offspring multibanding phenotype different from maternal profile ($MP_{offspring}$), and percent outcrossed offspring [$MP_{offspring}/(MP_{maternal} + MP_{offspring})$]* 100.

Population	Seed Source	$MP_{maternal}$	$MP_{offspring}$	Percent Outcrossed
Site 1	Non-Illinois	4	26	87
Site 2	West	4	72	95
	East	13	19	59
Site 3	Overall	17	91	84
	Non-Illinois	8	31	79
	Illinois	4	16	80
	Overall	12	47	80

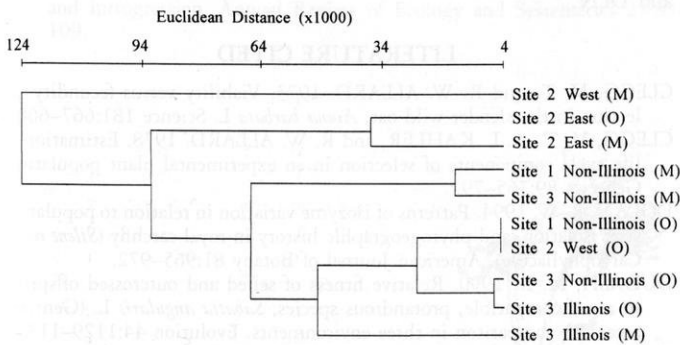


Fig. 2. Cluster analysis of Euclidean distances among populations based on isozyme band frequencies. Maternal sample (M) and offspring sample (O).

The ratio of MP /maternal plants with offspring increased by 33% in the non-Illinois subpopulation while the Illinois subpopulation was unchanged.

Genetic Structure

Mantel's tests indicated no relationship between geographic distance and genetic similarity within Site 1 ($Z = 0.39, P = 0.28$) and Site 2 ($Z = 0.01, P = 0.41$). There was a significant negative association ($Z = -0.28, P < 0.05$) in Site 3, which suggested a decrease in genetic similarity as the distance between plants increased. This result was not surprising given that Site 3 contained individuals derived from both non-Illinois and local Illinois seed.

Outcrossing Rates

The average population level outcrossing estimates ranged from 80% (Site 3) to 87% (Site 1) (Table 2). Site 2 estimates varied between 95% from the West transect that was located adjacent to the non-Illinois population, to 59% in the East transect (Table 2). The

outcrossing estimates for the Site 3 non-Illinois and Illinois subpopulations were 79% and 80%, respectively.

Population Relationships

The genetic relationships among the Goose Lake Prairie populations (maternal and offspring) were investigated using band frequency data and UPGMA cluster analysis (Fig. 2). The maternal non-Illinois populations grouped together, indicating that the genetic distinctiveness of the original non-Illinois source populations was maintained even after years of cultivation in Illinois.

Offspring from Site 1 and the West transect of Site 2 grouped together, even though the maternal populations were different. The close proximity of the non-Illinois population, from which Site 1 was sampled, and the West transect of Site 2 suggested that pollen from Site 1 was responsible for gene flow into the West transect of Site 2, as reflected by offspring phenotypes. Similarly, the non-Illinois and Illinois offspring of Site 3 clustered together. In both situations, there was a non-Illinois population planted adjacent to an Illinois population. All offspring populations grouped together except for the East transect of Site 2, which grouped with its maternal source. The local Site 3 maternal sample was somewhat distantly associated with the mainly offspring cluster.

Plant Performance

Non-Illinois *A. gerardii* plants were consistently shorter, produced fewer culms, and fewer infructescences than plants of Illinois origin (Table 3). In addition to the difference in plant performance, the non-Illinois plants were more frequently damaged by insects (23%) and matured later in the growing season than the Illinois plants (Table 3).

DISCUSSION

Populations established by seed, as with these restored populations, are expected to consist of a large number of randomly distributed genotypes (Ellstrand and Roose 1987). Our results are consis-

Table 3. Mean (± 1 SE) plant performance measures of big bluestem originally from Illinois and non-Illinois seed sources growing in Site 1 and Site 3.

Source	n	Height (cm)	Culms	Inflorescences	Insect Damage	Green
Non-Illinois	44	176.0 (3.50)	1.7 (0.20)	10.7 (1.20)	0.23 (0.06)	0.50 (0.08)
Illinois	15	243.7 (3.30)	11.2 (1.30)	63.1 (11.80)	0.00 (0.00)	0.00 (0.00)

*All comparisons within columns were significantly different at $P < 0.05$

tent with earlier studies in showing that the established (maternal) and offspring populations of *A. gerardii* are genetically diverse (Gustafson et al. 1999, Gustafson 2000). The oldest restored population, at 22 years since establishment, had the highest genetic diversity estimates. Several studies of grassland species have demonstrated an increase in viability associated with increased heterozygosity, which has been interpreted as selection against homozygosity (Clegg and Allard 1973, Schaal and Levin 1976, Clegg et al. 1978, Ritland and Ganders 1987, Dudash 1990, Fenster 1991). By removing the homozygous individuals from the population, selection would effectively increase the proportion of heterozygous individuals in the population over time. While we are unable to directly address questions of change in genetic diversity over time, this study does provide the baseline isozyme diversity estimates that can be compared to future genetic sampling of these restored populations. These baseline genetic data are essential for investigating fundamental biological questions under field conditions, such as change in genetic diversity over time.

Genetic structuring in our populations occurred only in Site 3, which consisted of two adjacent subpopulations of different origin (non-Illinois and Illinois). Genetically structured plant populations have been shown to have lower outcrossing rates and lower fitness relative to non-structured populations (Ennos and Clegg 1982, Ellstrand and Foster 1983, Dudash 1990, Fenster 1991). However, our structured population did not have any appreciable decrease in outcrossing rates relative to the non-structured populations. In this case, genetic structuring was due to the planting of non-Illinois and Illinois *A. gerardii* in adjacent areas and not a nonrandom distribution of individuals related by descent.

The established Illinois and non-Illinois populations growing in the field seemed to maintain their genetic identity even though 4/5 of offspring groups sampled were not associated with their maternal populations. Native *A. gerardii* populations are maintained almost exclusively by vegetative propagation (Hartnett 1989) despite a seed rain of ca. 3000 seeds m² in native populations (Foster and Gross 1997). The persistence of the non-Illinois populations through vegetative reproduction of rhizomes and new tillers could explain why they maintained their genetic integrity for more than 20 years. However, the seed cohort produced from these Illinois and non-Illinois plants indicates panmixia among these genetically different source populations. This result is significant because it suggests that seed collected from Illinois source populations does not provide a guarantee of a sample of exclusively Illinois genotypes.

Non-Illinois *A. gerardii* plants were consistently shorter, produced fewer culms and inflorescences than the Illinois *A. gerardii* plants. In addition, these non-Illinois plants were more prone to insect damage and matured later in the season than the local plants, suggesting morphological and phenological differences between the two types. These results were consistent with McMillan (1959); he found that *A. gerardii* from the western Great Plains were shorter and matured at a different time than the eastern ecotypes. The fact that the oldest non-Illinois population (Site 1) had the highest diversity estimates and has persisted for 22 years demonstrates that western cultivars *A. gerardii* can grow in northeastern Illinois.

A concern of restoration ecologists involves the choice of seed (local, non-local, cultivar) sources with respect to its adaptedness (Montalvo et al. 1997, Lesica and Allendorf 1999). Local adaptations can promote higher fitness under the specific ecological conditions of a site (Linhart and Grant 1996). However, the results of this study suggest that seed collected locally may not be of the local genotype if gene flow from a non-local or cultivar population has occurred. Documentation of the location of the donor seed source populations would provide researchers an opportunity to empirically determine the genetic identity and diversity of these donor populations. Future

studies documenting the change in genetic diversity over time and fitness differences among non-Illinois, Illinois, and intraspecific hybrids are needed to address the potential long-term fitness of these restored populations.

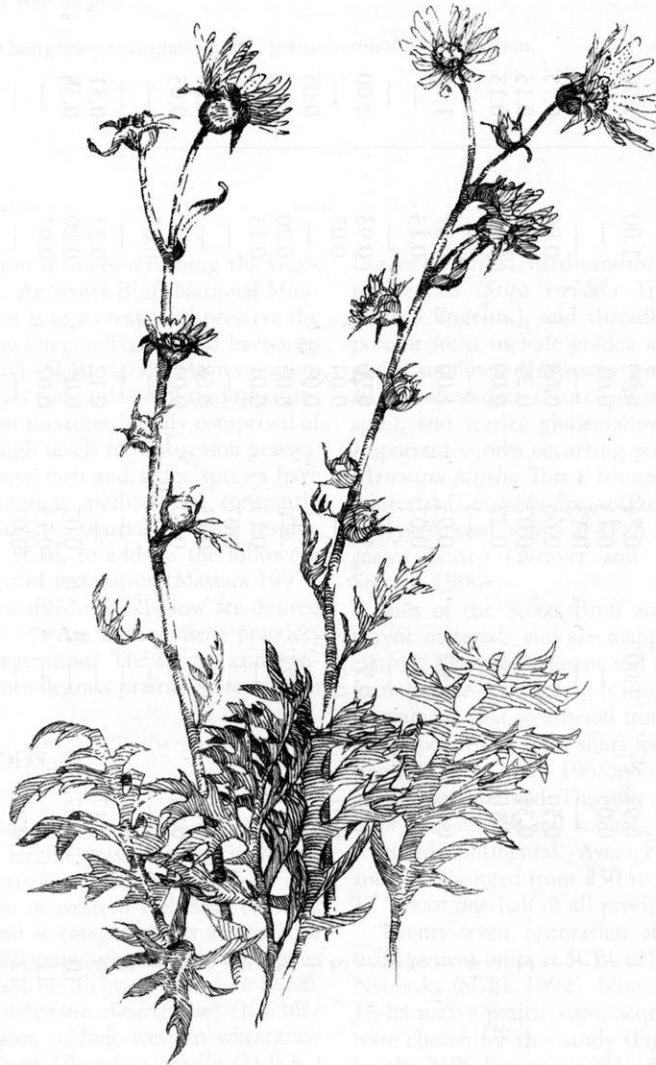
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Evaluation of Grassland Restoration at Scotts Bluff National Monument

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Efforts to restore and maintain presettlement vegetation at Scotts Bluff National Monument (SCBL) began in 1919 when the park was established in western Nebraska. Planting native seed, using prescribed fire, and controlling woody and weedy species have been part of management since the 1970s. In this study, nine restoration sites were compared with two native prairies to evaluate restoration success at SCBL.

Species composition of restoration sites and vegetation history at SCBL indicated that early restoration efforts failed to restore presettlement vegetation. Plant cover was adequate to protect soil from wind and water erosion. However, ordination showed that later efforts came closer to attaining native wheatgrass-needlegrass prairie species composition than did early approaches to restoration. In 1999, mean frequency of native cool-season perennial grasses of early plantings conducted in 1970–80s was lower (51–67%) than either that in adjacent native prairies (100%) or that in later 1997 plantings (97%). Other than an increase in native cool-season grasses and perennial forbs on some sites, species composition of restoration sites was relatively stable between 1993–99. Improvements in restoration results likely reflected changes in seed mixtures and planting methods. Precipitation had a greater effect on the quality of later restorations than early restorations.

INDEX DESCRIPTORS: wheatgrass-needlegrass prairie, prairie restoration, ordination.

By definition, vegetation restoration involves returning the vegetation to its former or original state. At Scotts Bluff National Monument (SCBL), the goal of restoration is to recreate and preserve the prairie as settlers travelling along the Oregon Trail would have seen it during the period of 1845 to 1865 (SCBL 1992). As restoration efforts have proceeded at SCBL, species composition of seed mixtures used in restorations has changed from mixtures heavily comprised of warm-season grasses to those with high levels of cool-season grasses. In addition, efforts to introduce native forb and sedge species have increased over time. Because restoration methods are constantly evolving at SCBL, assessment of sites is essential to track results. Vegetation monitoring was used at SCBL to address the following three questions related to evaluations of restoration (Masters 1997): (1) What species have successfully established? (2) How are desired species responding to management? (3) Are management practices effective in controlling unwanted vegetation? The species composition of two local native wheatgrass-needlegrass prairies were used to assess restoration success at SCBL.

METHODS

Study Area

SCBL lies within the central portion of the northern mixed prairie of the High Plains. It is one of the largest grassland associations in North America (Weaver and Albertson 1956, Stubbendieck and Willson 1986). The grassland region of western Nebraska contains both midgrasses and shortgrasses and is categorized as a mosaic of grama-buffalograss (*Bouteloua-Buchlöe*), grama-needlegrass-wheatgrass (*Bouteloua-Stipa-Agropyron*), wheatgrass-needlegrass (*Agropyron-Stipa*), and sandsage-bluestem prairies (*Artemisia-Andropogon*) (Küchler 1964). Dominant species of the region include western wheatgrass (*Agropyron smithii* Rydb.)¹, blue grama [*Bouteloua gracilis* (H.B.K.)

Lag. ex Griffiths], needleandthread (*Stipa comata* Trin. & Rupr.), green needlegrass (*Stipa viridula* Trin.), buffalograss [*Buchlöe dactyloides* (Nutt.) Engelm.], and threadleaf sedge (*Carex filifolia* Nutt.). Important forbs include golden aster [*Chrysopsis villosa* (Pursh) Nutt.], plains sunflower (*Helianthus petiolaris* Nutt.), prairie coneflower [*Ratibida columnifera* (Nutt.) Woot. & Standl.], goldenrods (*Solidago* spp.), and scarlet globemallow [*Sphaeralcea coccinea* (Pursh) Rydb.]. Important shrubs occurring within this area include sand sagebrush (*Artemisia filifolia* Torr.), fringed sagebrush (*Artemisia frigida* Willd.), winterfat [*Ceratoides lanata* (Pursh) J. T. Howell], rubber rabbitbrush [*Chrysothamnus nauseosus* (Pall.) Britt.], and small soapweed (*Yucca glauca* Nutt.) (Weaver and Albertson 1956, Wendtland 1993, Stumpf 1996).

Soils of the Scotts Bluff area are derived from sandy colluvium parent materials and are mapped as a Mitchell-Keith-Epping association. The predominant soil type at the study sites is Mitchell silt loam [coarse-silty, mixed (calcareous), mesic Typic Ustorthent] formed in material that weathered from Brule siltstone and was transported and deposited to form short foot slopes or broad, nearly level, basin-like fans (Yost et al. 1968). Soils are deep and well-drained or moderately well-drained. The soils are immature with a medium-textured layer beneath the soil surface. The climate of Scotts Bluff County is semiarid continental. Average annual precipitation between 1970 and 1999 ranged from 230 to 630 mm and averaged 416 mm (Fig. 1). About one-half of all precipitation occurs between May and July.

Twenty-seven restoration areas have been identified within 12 management units at SCBL (41° 50.5'N, 103° 41.6'W) near Gering, Nebraska (SCBL 1992). Nine 10 to 28-ha restoration sites and two 16-ha native prairie sites, acquired at the park's inception in 1919, were chosen for this study (Fig. 2). Restoration Sites were acquired by the NPS between 1971 and 1990 (Table 1). A cover crop was planted at several sites prior to restoration efforts. In addition, physical barriers were removed and exotic woody vegetation cut and removed before Restoration Sites were planted.

¹ Scientific names generally follow the Great Plains Flora Association (1986), but are updated with more recent names when appropriate.

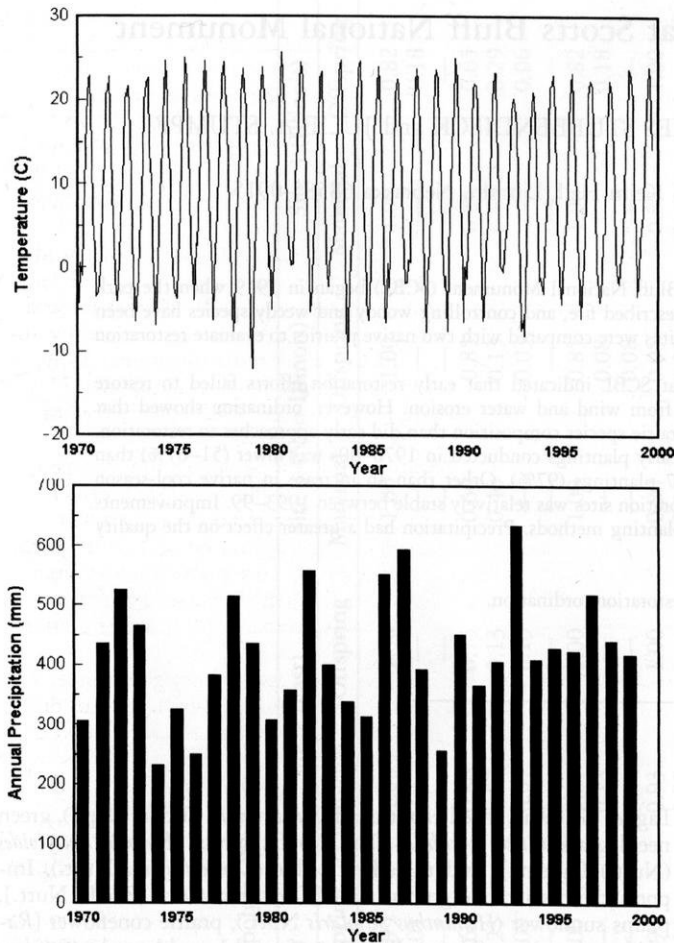


Fig. 1. Mean monthly temperature and total annual precipitation at SCBL between 1970–1999 (NOAA 1970–1999).

The 4.80 to 6.84 kg ha⁻¹ seed mixture evolved from those used in early restoration efforts comprised primarily of warm-season grass species to later mixtures comprised primarily of cool-season grasses (Table 2). In addition, native forb and shrub species have been planted in a number of the Restoration sites. In 1996 and 1998, transplants and plugs of threadleaf sedge were planted in experimental plots located in Sites 8 and 9. Threadleaf sedge has not been seeded in any of the restoration because seed is not commercially available.

Wildfires have been rare, but Restoration Sites 4 and 12 were burned in small wildfires in 1980 and 1989, respectively. In the spring of 1983, prescribed burning was introduced as a management tool with an 334-ha burn southeast of the headquarters and west of Mitchell Pass. Since then, other units have been burned as part of management. Restoration Sites 2 and 15 were burned in 1998 and 1985, respectively. Grazing has not been used in prairie management since World War II.

Vegetation Sampling

Vegetation composition data collected in 1993, 1994, 1998, and 1999 were used to compare restoration sites to native prairie sites. Success of restoration was first measured by how similar vegetation at restoration sites is to vegetation in native prairie sites. Restoration success was then evaluated according to whether vegetation composition of restoration sites was becoming more or less similar to that

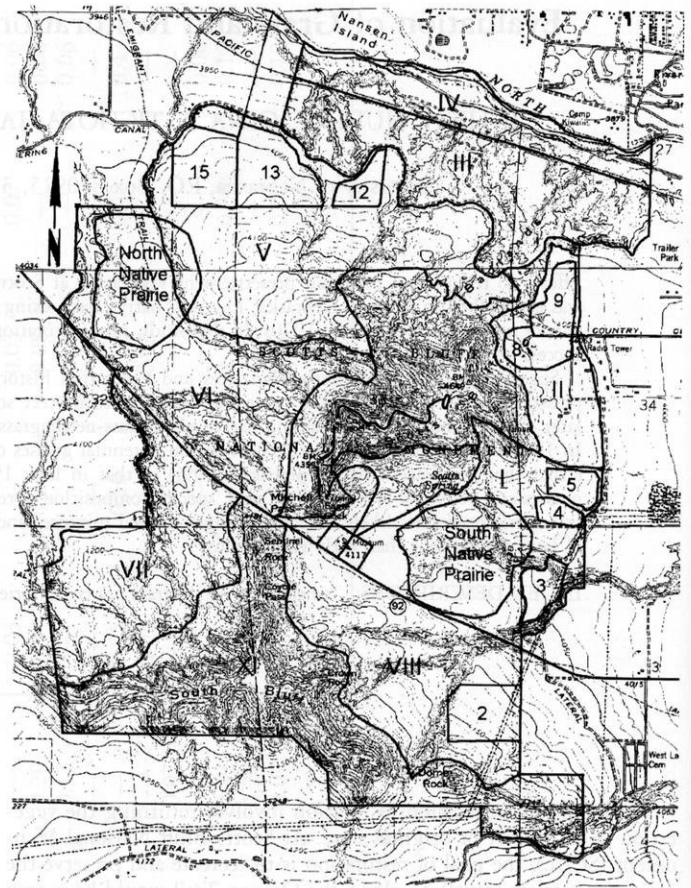


Fig. 2. Management units, Restoration Sites and Native Prairie Sites at SCBL.

of native prairie sites from 1993–94 to 1998–99. Data collected on vegetation composition in 1998 and 1999 from new restoration sites (8 and 9) was used to assess initial success of these restorations and to serve as the baseline for long-term evaluations.

Species frequency at each site was determined using a 0.25 m² rectangular quadrat randomly located within the site. The number of samples taken at a site reflected the area of the site (Fig. 2). At least 100 samples were taken from each site with an average of 12 samples ha⁻¹. Small study plots in Restoration Sites 8 and 9 established in 1996 and 1998 to examine methods of restoring threadleaf sedge were excluded from the vegetation surveys. Each species was assigned to one of eight vegetation classes: (1) sedges, (2) native warm-season perennial grasses, (3) native cool-season perennial grasses, (4) exotic cool-season perennial grasses, (5) annual grasses, (6) perennial forbs, (7) annual/biennial forbs, and (8) shrubs/succulents.

Percent frequencies from 1998 and 1999 for each site were summed by species category. If the summed frequency value for a given species category exceeded 100%, a value of 100% was assumed. This procedure likely overestimated the cover for some species categories when several species of the given category were likely to occur in some quadrats while none occurred in others. Comparing frequency values of species categories calculated in this manner with values tabulated by site indicated that this calculation slightly overestimated frequency for most forb species, but produced comparable results for warm-season grasses and sedges (Stumpf 1996).

Table 1. Size, restoration goal, year acquired, and management of SCBL Sites.

Site	Size (ha)	Restoration Goal	Year Acquired	Management History
2	16.1	Wheatgrass-needlegrass prairie	1979	Dryland wheat production prior to acquisition. Cover crop of sorghum planted in the Spring of 1980 before seeding to native prairie species.
3	6.4	Wheatgrass-needlegrass prairie	1981	Irrigated cropping prior to acquisition Millet planted in 1987 and 1988. Fall 1988: mowed and planted to commercial seed mixture of native grasses followed by application of dicamba in summer 1989.
4, 5	8.1		1971	Dryland farming prior to acquisition May have been seeded with a native prairie grass seed mixture.
8	8.1	Presettlement vegetation	1973	Golf course prior to acquisition. In 1984, concrete and asphalt removed. Millet planted in 1987 and 1988. Summer 1989, light application of dicamba herbicide applied and mowed 6 weeks later, April 1997, native grasses and forbs planted. December 1997, native grasses planted.
9	14.9	Presettlement vegetation	<1990	Prior headquarters for local golf course. Summer 1989, light application of dicamba herbicide applied and mowed 6 weeks later. December 1997, native grasses and forbs planted.
12	9.6	Presettlement vegetation	1974	Previously leveled for wheat production. Fall 1989, berms recontoured and native grass seed drilled.
13	27.8	Presettlement vegetation	1974	Previously leveled for wheat production. Site conditions suggest a mixture of native grasses planted after acquisition.
15	19.7	Presettlement vegetation	1974	Previously leveled for wheat production. Sometime in the 1980s following acquisition, site was seeded to cover crop and then seeded with a mixture of native grasses.
NN, NS	≥16.1	Maintain current vegetation	1919	Acquired with initial park establishment.

Statistical Analysis

To place similar sites into groups, Detrended Correspondence Analysis (DCA) was used with rare species down-weighted (Hill 1979) using PC-ORD 2.0 (McCune and Mefford 1995). In addition, species with a frequency <10% when summed over all locations and years were deleted in order to ensure ordination results were not skewed by uncommon species. Relative plot ordination results were plotted for the three axes calculated, and DCA scores for species were tabulated. To normalize data, the square root was taken of the summed frequency values, and these were arcsine transformed before analysis using the General Linear Models procedure of SAS by sampling period (1993–94, 1998–99) and by the four site groups determined from DCA analysis. A complete randomized block design was employed with species category, site group, and the interaction between species category and site group. For presentation, means were back transformed into percentages.

RESULTS

Plotting relative ordination scores of study sites from DCA showed that sites can be separated into four groups: Group 1 included Native-North and Native-South Sites; Group 2 included Restoration Sites 8 and 9; Group 3 included Restoration Sites 3, 12, and 13; Group 4 included Restoration Sites 2, 4, 5, and 15 (Fig. 3). Species associated with lower values of Axis 1 included threadleaf sedge, sixweeks fescue [*Vulpia octiflora* (Walt.) Rydb.], and Hood's phlox (*Phlox hoodii* Rich.) and were relatively frequent in Group 1 native prairie sites (Table 3). These species were most frequently found in Group 1 sites. In contrast, species associated with upper values of Axis 1 included little bluestem [*Schizachyrium scoparium* (Michx.) Nash], sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.], and yellow sweetclover [*Melilotus officinalis* (L.) Pall.]. These species were most frequent in Group 4 Sites. Groups 2 and 3 had intermediate scores of DCA factor 2.

Table 2. Seed mixtures planted at restoration sites of Scotts Bluff National Monument.

Species	Restoration Site/s and year/s Seed Mixture Planted									
	8-1997		9-1997		3,12,13-1980s		2,15-1980s		2-1998	
	kg ha ⁻¹	%	kg ha ⁻¹	%	kg ha ⁻¹	%	kg ha ⁻¹	%	kg ha ⁻¹	%
COOL-SEASON GRASSES										
Western wheatgrass	1.11	23	1.06	16	1.68	25	1.68	25	0.06	11
Junegrass	0.02	tr	0.02	tr	—	—	—	—	0.24	tr
Needleandthread	2.80	58	2.80	42	—	—	—	—	0.32	57
Green needlegrass	—	—	—	—	0.67	10	0.67	10	—	—
WARM-SEASON GRASSES										
Blue grama	0.29	6	0.29	4	0.34	5	0.34	5	—	—
Sideoats grama	0.34	7	0.34	5	0.90	13	0.90	13	—	—
Buffalograss	0.23	5	—	—	2.24	33	2.24	33	—	—
Prairie sandgrass	—	—	0.23	4	0.67	10	0.67	10	—	—
Little bluestem	—	—	0.00	0	0.34	5	0.34	5	—	—
NATIVE PERENNIAL FORBS										
Dotted gayfeather	—	—	0.23	3	—	—	—	—	0.01	2
Prairie coneflower	—	—	0.02	tr	—	—	—	—	0.02	4
Scarlet globemallow	—	—	0.28	4	—	—	—	—	0.03	6
Arroyo golden banner	—	—	0.65	10	—	—	—	—	0.01	2
SHRUBS AND SUCCULENTS										
Winterfat	—	—	0.33	5	—	—	—	—	—	—
Woods rose	—	—	0.37	6	—	—	—	—	0.04	8

Groups 1 and 2 had lower scores of the second DCA factor (Axis 2) than Groups 3 and 4 (Fig. 3). Species associated with lower values of Axis 2 included needleleaf sedge (*Carex eleocharis* Bailey), scarlet globemallow, and threadleaf sedge. In contrast, species associated with upper values of Axis 2 included crested wheatgrass, [*Agropyron cristatum* (L.) Gaertn.], red three-awn, [*Aristida purpurea* (Nutt.)] and Kochia [*Kochia scoparia* (L.) Schrad.].

Group 2 Sites had the highest scores of the third DCA factor (Axis 3), Groups 3 and 4 Sites had intermediate scores of the third DCA factor, and Group 1 had the lowest score of the third DCA factor (Fig. 3). Species associated with lower values of Axis 3 included threadleaf sedge, crested wheatgrass, plains milkweed, [*Asclepias pumila* (A. Gray) Vail], and winterfat. In contrast, species associated with upper values of Axis 3 included field bindweed (*Convolvulus arvensis* L.), smooth brome (*Bromus inermis* Leys.), downy brome (*Bromus tectorum* L.), Russian thistle (*Salsola iberica* Sennen & Pau), and sand dropseed [*Sporobolus cryptandrus* (Torr.) A. Gray].

Group 1 Sites

The native prairie sites, Group 1 Sites, were distinguished from all the other groups by their outstanding cover of threadleaf sedge and needleandthread. In addition, Group 1 Sites had a high frequency of blue grama, prairie sandreed [*Calamovilfa longifolia* (Hook.) Scribn.], scarlet globemallow, downy brome, Japanese brome (*Bromus japonicus* Thunb. ex Murr.), and skeletonweed [*Lygodesmia juncea* (Pursh) Hook.]. Throughout the study, Group 1 Sites maintained a high frequency of native cool-season grasses, sedges, perennial forbs, and native warm-season perennial grasses (Fig. 4). The Group 1 native prairie sites had higher sedge frequency than all other groups in all years (Table 3). In all but 1993, perennial forb frequency was highest in Group 1 plots (Fig. 5). Frequency of annual/biennial forbs dropped significantly from 98% in 1993 to 22–29% in subsequent surveys. Russian thistle, an exotic species, accounted for most of this drop in annual/biennial forb frequency. In addition, plains sunflower, Redowski's stickseed [*Lappula redowski* (Hornem.) Greene], and com-

mon evening primrose (*Oenothera biennis* L.), the primary native annual/biennial forbs, also decreased in frequency. In the Native North site, frequency of needleandthread decreased; frequency of western wheatgrass, Japanese brome, and winterfat increased; and frequency of threadleaf sedge remained nearly constant. In contrast, frequencies of threadleaf sedge and needleandthread increased slightly in the Native South site. Frequency of western wheatgrass declined in 1998, but partially recovered in 1999. Blue grama frequency was 13% or higher in all years surveyed for both native sites.

Group 2 Sites

Group 2 Sites (Restoration Sites 8, and 9) were characterized by western wheatgrass, needleandthread, green needlegrass, sand dropseed, and downy brome (Table 3). Frequency of Japanese brome was variable, but relatively little (<10%) was present on Restoration Sites 8 and 9. According to DCA analysis, composition of Group 2 Sites was most similar to that of the native prairies in the Group 1 Sites. Similarities were due mainly to the relatively frequent occurrence of blue grama, sideoats grama, western wheatgrass, needleandthread, prairie sandreed, and scarlet globemallow with only scattered stands of threadleaf sedge and needleleaf sedge observed at Site 9.

Group 3 Sites

Group 3 Sites (Restoration Sites 3, 12, and 13) had high frequencies of western wheatgrass, crested wheatgrass, downy brome, red three-awn, sand dropseed, needleandthread, green needlegrass, Japanese brome, and Russian thistle (Table 3). Perennial forbs frequently found in Group 3 Sites included native western ragweed (*Ambrosia psilostachya* DC.), skeletonweed, clammy groundcherry (*Physalis heterophylla* Nees.), and the exotic field bindweed. Additional common forbs of Site 13 included Texas croton [*Croton texensis* (Kl.) Muell. Arg.], Kochia, and Russian thistle. In all years, Group 3 plots had a frequency of native cool-season grasses comparable to that of Group 1, the native prairie sites (Fig. 4). Downy brome and

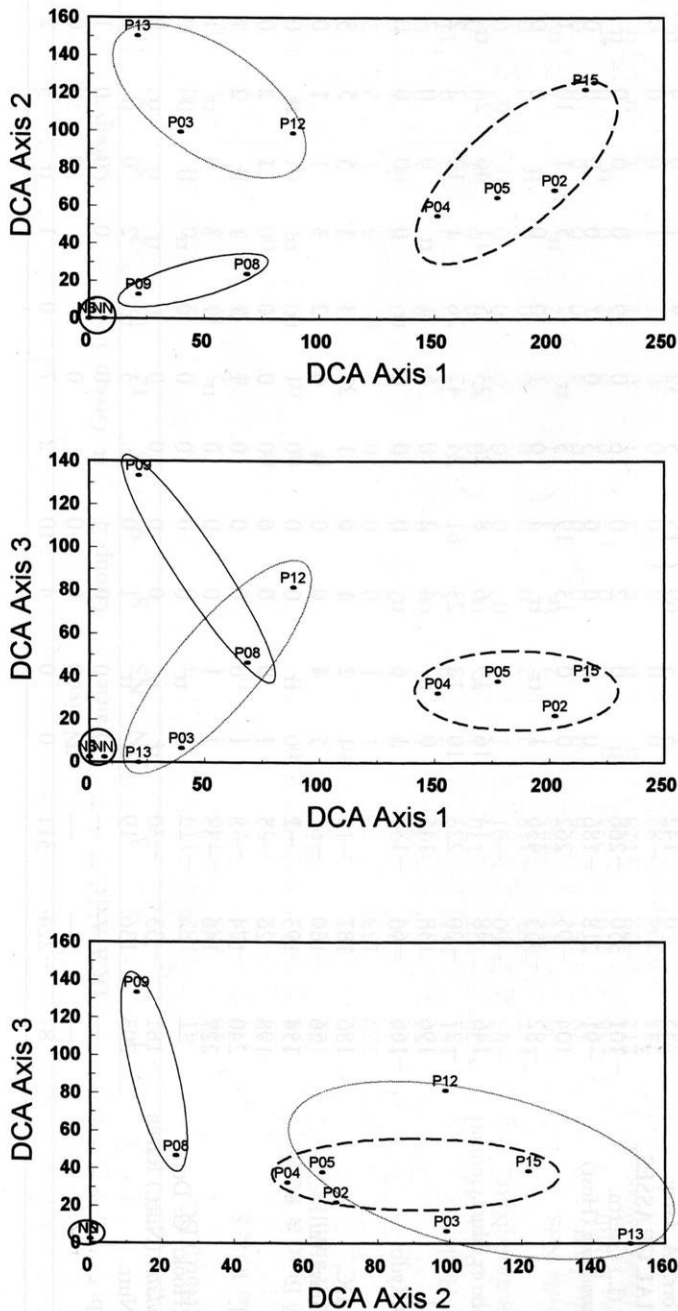


Fig. 3. Restoration Sites and native prairies graphed by DCA ordination scores. Labels designate Restoration Site field number or Native Prairie Site (N = north; S = south). A—First and second DCA ordination scores. B—First and third DCA ordination scores. C—Second and third DCA ordination scores.

Japanese brome accounted for the high frequency of annual grasses of Group 3 Sites, while exotic species kochia and Russian thistle accounted for the high annual/biennial forb frequency of Group 3 Sites.

Group 4 Sites

Group 4 Sites (Restoration Sites 2, 4, 5, and 15) were characterized by having a high cover of sideoats grama, little bluestem, and

sweet clovers (*Melilotus* spp.) (Table 3). In addition, Sites 4 and 5 had relatively large amounts of prairie sandreed, needleandthread, and Japanese brome. Occurrence of native warm-season perennial grasses remained high throughout the course of the study for Group 4. In all years surveyed, frequency of native warm-season perennial grasses was significantly higher for Group 4 than any other group of sites (Fig. 4). Frequency of annual/biennial forbs decreased with time, while shrub/succulent frequency increased (Fig. 5). The exotic species Russian thistle and yellow sweetclover accounted for most of the decrease in annual/biennial forbs frequency. Increasing shrub frequency in Group 4 Sites was due primarily to small increases in winterfat and small soapweed on some of the sites, while frequency of fringed sagebrush decreased on Site 4.

DISCUSSION

Examination of vegetation composition of restoration sites together with the restoration history at SCBL suggested that changes in both planting method and seed mixture had greatly improved prairie restoration. Of all restoration groups, Group 2 Sites had a species composition most comparable to the Group 1 native prairie sites. On at least one of the Group 4 Restoration Sites, a native grass mixture comprised primarily by buffalograss, western wheatgrass, and sideoats grama was directly sown by drilling. In contrast, on two of the Group 2 Restoration Sites, 2 and 15, cover crops were sown before fields were planted with a mixture of native grass species. Although needleandthread was later seeded at Site 2, little was observed in 1999. Lastly, Site 3 of Restoration Group 3 Sites was sown with a native prairie mixture following two years of a cover crop of millet (*Panicum miliaceum* L.). The other two Sites, 8 and 9, of Restoration Group 2 were planted with more complex seed mixtures with a higher composition of needleandthread and forb species. Forbs were not seeded with the grasses but were hand-broadcast in small, localized areas within the larger Restoration Sites.

All Group 4 Restoration Sites had a higher frequency of native warm-season grasses, particularly sideoats grama and little bluestem, than Group 1 native prairie sites. Although the frequencies of blue grama and prairie sandreed of Group 2 Restoration Sites were similar to those of native prairie sites, Group 2 Sites had a higher frequency of sand dropseed than native prairie sites. All native warm-season grasses, except red three-awn, were found in greater abundance in one or more groups of Restoration Sites than in native prairies. Group 4 Restoration Sites had greater amounts of red three-awn and sand dropseed but lower amounts of blue grama and prairie sandreed than native prairie sites. Lastly, none of the restoration sites had a significant level of threadleaf sedge.

Establishing frequencies of needleandthread comparable to that of native prairie was problematic for all groups and sites of restoration, while the frequency of western wheatgrass on most restoration sites was comparable to that of native prairies. In 1999, the frequency of all native cool-season grasses averaged 94, 84, and 51% in Groups 2, 3, and 4 respectively. The highest frequency of needleandthread observed at restoration sites in 1999 was 56% at Site 8. In contrast, the frequency of all native cool-season grasses averaged 100% in all years at native prairie sites, and the frequency of needleandthread in 1999 ranged from 71 to 84%. Sites acquired in the early 1970s tended to have greater amounts of needleandthread than green needlegrass, while the reverse held true at sites acquired in the 1990s. These differences likely reflected the replacement of green needlegrass with needleandthread in seed mixtures used to plant restoration sites.

Examination of vegetation composition of restoration sites together with the vegetation history at SCBL suggested that some of the

Table 3. Species DCA scores and average frequency by Restoration Grouping and Restoration Site.

Species	DCA Axis			Native Prairie		Group 2		Group 3			Group 4			
	1	2	3	NN	NS	8	9	3	12	13	2	4	5	15
SEDGES														
Needleleaf sedge, <i>Carex eleocharis</i> Bailey	-153	-342	256	2	1	0	2	0	0	0	0	0	0	0
Threadleaf sedge, <i>Carex filifolia</i> Nutt.	-166	-94	-122	72	64	0	1	0	0	0	0	tr	0	0
NATIVE COOL-SEASON PERENNIAL GRASSES														
Western wheatgrass, <i>Agropyron smithii</i> Rydb.	-8	127	54	42	56	46	54	89	20	62	30	17	8	6
Canada Wildrye, <i>Elymus canadensis</i> L.	168	-52	146	0	0	1	1	1	0	0	tr	1	1	tr
Prairie junegrass, <i>Koeleria macrantha</i> (Ledeb.) Schult.	141	-20	-27	2	1	1	0	0	0	0	tr	1	2	0
Indian ricegrass, <i>Oryzopsis hymenoides</i> (R. & S.) Ricker	141	107	1	tr	tr	2	0	tr	1	tr	0	tr	1	tr
Squirreltail, <i>Sitanion hystrix</i> (Nutt.) J. G. Smith	233	61	98	0	0	tr	1	1	1	0	0	5	8	tr
Needleandthread, <i>Stipa comata</i> Trin. & Rupr.	-3	-30	-8	81	78	46	16	2	21	10	3	30	28	0
Green needlegrass, <i>Stipa viridula</i> Trin.	108	56	-62	0	0	18	0	28	1	2	13	0	tr	0
NATIVE WARM-SEASON PERENNIAL GRASSES														
Sand bluestem, <i>Andropogon hallii</i> Hack.	-93	-90	-108	2	1	0	0	0	0	0	tr	0	0	0
Red three-awn, <i>Aristida purpurea</i> (Nutt.)	131	214	-30	1	1	1	0	2	32	10	1	5	10	1
Sideoats grama, <i>Bouteloua curtipendula</i> (Michx.) Torr.	283	116	29	6	4	20	1	4	2	3	82	50	47	98
Blue grama, <i>Bouteloua gracilis</i> (H.B.K.) Lag. ex. Griffiths	69	-40	-20	22	22	27	3	6	tr	tr	4	18	3	7
Buffalograss, <i>Buchloe dactyloides</i> (Nutt.) Englem.	63	114	-54	tr	tr	6	0	12	5	1	2	1	1	1
Prairie sandgrass, <i>Calamovilfa longifolia</i> (Hook.) Scribn.	194	25	12	15	9	12	2	tr	2	1	7	45	32	2
Little bluestem, <i>Schizachyrium scoparium</i> (Michx.) Nash	285	26	39	2	1	tr	0	tr	1	tr	60	40	52	8
Sand dropseed, <i>Sporobolus cryptandrus</i> (Torr.) A. Gray	55	0	142	3	3	69	15	5	32	7	1	9	9	tr
EXOTIC COOL-SEASON PERENNIAL GRASSES														
Crested wheatgrass, <i>Agropyron cristatum</i> (L.) Gaertn.	-101	350	-266	tr	0	2	0	16	0	39	0	0	0	tr
Intermediate wheatgrass, <i>Agropyron intermedium</i> (Host)	-91	218	-186	0	0	0	0	3	0	1	0	0	0	0
Smooth brome, <i>Bromus inermis</i> Leyss.	104	-95	262	0	0	13	19	3	tr	7	5	1	10	1
Kentucky blugrass, <i>Poa pratensis</i> L.	-82	-455	436	1	tr	tr	4	0	1	0	0	tr	0	0
ANNUAL GRASSES														
Japanese brome, <i>Bromus japonicus</i> Thunb. ex Murr.	146	48	14	16	19	6	8	26	23	5	11	46	24	tr
Downy brome, <i>Bromus tectorium</i> L.	-27	-20	223	10	12	23	61	24	47	26	1	12	2	2
Common witchgrass, <i>Panicum capillare</i> L.	196	138	145	0	tr	4	2	0	5	1	tr	0	0	7
Sixweeks fescue, <i>Vulpia octoflora</i> (Walt.) Rydb.	-166	-64	-134	1	6	tr	0	0	0	tr	0	0	0	0
PERENNIAL FORBS														
Western ragweed, <i>Ambrosia psilostachya</i> DC.	156	187	4	1	2	1	0	1	24	3	1	5	5	3
Plains milkweed, <i>Asclepias pumila</i> (A. Gray) Vail	56	160	-67	5	4	0	0	tr	6	2	3	1	1	0
Showy milkweed, <i>Asclepias speciosa</i> Torr.	154	193	-2	0	tr	0	0	0	1	tr	tr	1	tr	0
Heath aster, <i>Aster ericoides</i> L.	198	26	-5	1	0	0	0	0	0	0	0	1	2	0
White prairie aster, <i>Aster falcatus</i> Lindl.	240	174	-8	1	0	0	0	0	1	1	1	tr	2	1
Aster species, <i>Aster</i> spp.	227	146	-33	1	1	0	0	0	tr	1	3	0	tr	1
Pliant milk-vetch, <i>Astragalus flexuosus</i> (Hook.) G. Don	—	—	—	2	tr	0	0	0	0	0	tr	0	0	0
Plains yellow primrose, <i>Calylophus serrulatus</i> (Nutt.) Raven	181	-33	-30	tr	tr	0	0	0	0	0	tr	tr	tr	0
Goldenaster, <i>Chrysopsis villosa</i> (Pursh) Nutt.	203	136	19	tr	tr	1	0	tr	3	tr	2	0	tr	1
Canada thistle, <i>Cirsium arvense</i> (L.) Scop.	—	—	—	0	0	0	1	tr	0	0	0	0	0	1
Platte thistle, <i>Cirsium canescens</i> Nutt.	—	—	—	tr	0	0	0	tr	0	tr	tr	0	0	0
Field, bindweed, <i>Convolvulus arvensis</i> L.	87	-224	311	0	0	4	10	2	7	0	1	tr	3	2

Table 3. Continued.

Species	DCA Axis			Native Prairie		Group 2		Group 3			Group 4				
	1	2	3	NN	NS	8	9	3	12	13	2	4	5	15	
Western wallflower, <i>Erysimum asperum</i> (Nutt.) DC.	41	182	-119	3	4	0	0	0	0	2	0	tr	0	3	
Spurge species, <i>Euphorbia</i> spp.	16	268	-146	3	1	0	0	2	5	10	1	2	1	tr	
Nuttall's evolvulus, <i>Evolvulus nuttallianus</i> R. & S.	4	-64	-21	1	tr	2	0	0	0	0	0	tr	0	0	
Scarlet gaura, <i>Gaura coccinea</i> Pursh	-33	-42	-58	4	8	2	1	tr	0	1	tr	2	1	0	
Snakeweed, <i>Gutierrezia sarothrae</i> (Pursh) Britt. & Rusby	238	-12	-1	tr	tr	0	0	tr	tr	0	1	tr	tr	0	
Cutleaf ironplant, <i>Haplopappus spinulosus</i> (Pursh) DC.	165	-31	-15	1	1	1	0	tr	0	0	1	1	1	0	
False boneset, <i>Kubnia eupatorioides</i> L.	189	201	-11	tr	1	0	1	1	4	3	2	2	5	2	
Blue lettuce, <i>Lactuca oblongifolia</i> Nutt.	229	133	2	1	1	0	0	0	2	tr	3	1	2	2	
Dotted gayfeather, <i>Liatris punctata</i> Hook.	133	-30	-2	0	1	2	0	0	0	0	0	tr	1	0	
Puccoon, <i>Lithospermum incisum</i> Lehm.	72	-40	-45	1	tr	tr	0	0	0	0	tr	1	0	0	
Skeletonweed, <i>Lygodesmia juncea</i> (Pursh) Hook.	151	161	-6	7	8	1	1	tr	24	2	4	3	0	11	
Narrowleaf four-o'clock, <i>Mirabilis linearis</i> (Pursh) Heimerl	-20	-171	170	1	tr	tr	1	0	tr	0	0	1	0	0	
Dotted beebalm, horsemint, <i>Monarda pectinata</i> Nutt.	-43	-60	-91	1	1	0	0	0	0	0	0	tr	tr	0	
Hood's phlox, <i>Pblox hoodii</i> Rich.	-137	-83	-118	2	2	0	0	0	0	0	0	tr	0	0	
Clammy groundcherry, <i>Physalis heterophylla</i> Nees.	25	111	173	1	2	tr	4	1	5	2	tr	1	1	tr	
Common groundcherry, <i>Physalis longifolia</i> Nutt.	79	181	76	0	0	0	0	0	4	0	0	0	0	0	
Virginia groundcherry <i>Physalis virginiana</i> P. Mill.	-58	219	225	tr	0	0	2	0	0	2	0	tr	0	tr	
Prairie coneflower, <i>Ratibida columnifera</i> (Nutt.) Woot. &	212	-59	128	tr	0	6	2	1	0	1	9	1	tr	tr	
Black-eyed Susan, <i>Rudbeckia hirta</i> L.	243	224	-82	0	0	0	0	0	0	1	1	0	0	0	
Missouri goldenrod, <i>Solidago missouriensis</i> Nutt.	232	22	4	1	tr	tr	0	tr	tr	0	2	tr	3	1	
Scarlet globemallow, <i>Sphaeralcea coccinea</i> (Pursh) Rydb.	-35	-140	131	28	34	8	16	1	4	2	4	10	4	1	
Hoary vervain <i>Verbena stricta</i> Vent.	197	-29	169	tr	tr	0	1	0	0	tr	tr	2	1	0	
ANNUAL FORBS															
Tumble pigweed, <i>Amaranthus albus</i> L.	278	206	-9	0	1	0	0	0	1	1	0	0	0	4	
Rough pigweed, <i>Amaranthus retroflexus</i> L.	122	142	104	0	tr	4	1	1	tr	1	0	0	0	2	
Common ragweed, <i>Ambrosia artemisiifolia</i> L.	-118	323	-255	tr	tr	0	0	1	0	1	0	0	0	0	
Musk thistle, <i>Carduus nutans</i> L.	-79	-546	489	0	0	1	2	0	0	0	0	0	0	0	
Goosefoot species, <i>Chenopodium</i> spp.	182	117	31	13	6	4	4	3	5	4	6	10	6	18	
Horseweed, <i>Conyza canadensis</i> (L.) Cronq.	163	276	-106	tr	0	0	0	0	2	3	tr	tr	tr	2	
Texas croton, <i>Croton texensis</i> (Kl.) Muell. Arg.	132	204	2	1	1	0	0	0	19	3	1	1	0	3	
Tansy mustard, <i>Descurainia pinnata</i> (Walt.) Britt.	4	220	-135	1	tr	tr	0	1	tr	1	0	0	0	1	
Flixweed, <i>Descurainia sophia</i> (L.) Webb ex Prantl	-107	6	-125	0	2	0	0	2	tr	0	0	0	0	0	
Ridge-seeded spurge, <i>Euphorbia glyptosperma</i> Engelm.	12	212	93	tr	1	1	2	tr	3	3	tr	1	0	tr	
Curly-top gumweed, <i>Grindelia squarrosa</i> (Pursh) Dun.	27	-70	21	0	0	2	0	0	0	0	0	0	0	0	
Common sunflower, <i>Helianthus annuus</i> L.	209	189	16	2	tr	1	1	0	0	3	1	5	6	3	
Plains sunflower, <i>Helianthus petiolaris</i> Nutt.	151	151	-27	0	2	1	0	tr	3	1	2	0	0	1	
Kochia, <i>Kochia scoparia</i> (L.) Schrad.	-1	193	27	tr	tr	7	9	24	7	15	0	1	3	4	
Prickly lettuce, <i>Lactuca serriola</i> L.	197	186	70	1	1	0	1	1	2	2	1	2	tr	4	
Redowski's stickseed, <i>Lappula redowski</i> (Hornem.) Greene	-55	-54	-105	tr	5	tr	0	1	0	0	tr	1	0	0	
Peppergrass, <i>Lepidium densiflorum</i> Schrad.	17	-80	-45	1	1	1	0	0	0	0	tr	0	0	0	
White sweetclover, <i>Melilotus alba</i> Medic.	277	-90	99	0	0	3	1	tr	0	0	12	0	0	0	
Yellow sweetclover, <i>Melilotus officinalis</i> (L.) Pall.	249	143	40	1	1	10	1	3	34	2	26	35	46	43	
Common evening primrose, <i>Oenothera biennis</i> L.	-109	-76	-109	4	3	0	0	0	0	0	0	1	0	0	
Knotweed, <i>Polygonum ramosissimum</i> Michx.	352	191	50	0	0	0	0	0	0	0	0	0	0	4	
Slimflower scurfpea, <i>Psoralea tenuiflora</i> Pursh.	138	-69	92	1	1	1	1	0	0	0	tr	1	1	1	
Russian thistle, <i>Salsola iberica</i> Sennen & Pau	41	107	145	22	11	12	32	25	42	24	3	16	16	6	

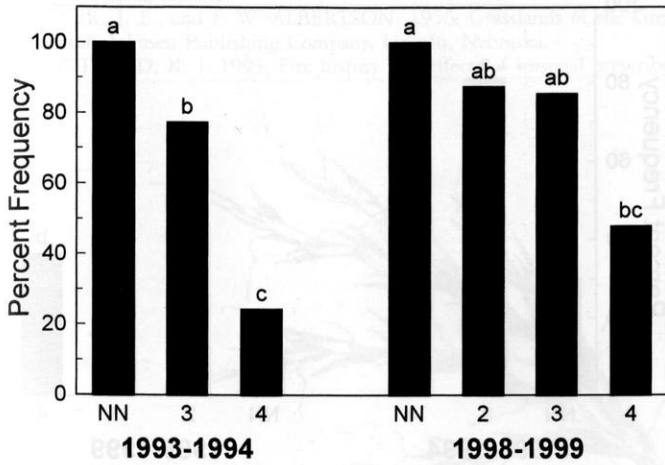
Table 3. Continued.

Species	DCA Axis			Native Prairie		Group 2		Group 3			Group 4				
	1	2	3	NN	NS	8	9	3	12	13	2	4	5	15	
Tumbling mustard, <i>Sisymbrium altissimum</i> L.	-9	249	-78	1	2	tr	1	tr	6	5	0	1	0	1	
Goat's beard, <i>Tragopogon dubius</i> Scop.	-11	276	-144	1	1	0	1	3	1	6	1	0	tr	1	
Prostrate vervain, <i>Verbena bracteata</i> Lag. & Rodr.	29	-59	16	0	tr	24	0	tr	tr	tr	0	tr	0	0	
SHRUBS AND SUCCULENTS															
Sand sagebrush, <i>Artemisia filifolia</i> Torr.	63	44	-61	1	2	0	0	0	1	tr	0	1	tr	tr	
Fringed sagebrush, <i>Artemisia frigida</i> Willd.	229	-27	17	1	2	2	1	3	1	0	14	4	5	0	
Winterfat, <i>Caratoides lanata</i> (Pursh) Howell	83	-10	-65	10	14	3	0	13	tr	0	3	13	7	0	
Rubber rabbitbrush, <i>Chrysothamnus nauseosus</i> (Pall.)	75	37	-15	0	tr	tr	1	7	3	0	2	0	tr	0	
Plains pricklypear, <i>Opuntia macrorhiza</i> Englem.	—	—	—	1	tr	0	0	0	tr	0	0	tr	0	tr	
Plains pricklypear, <i>Opuntia polyacantha</i> Haw.	-73	122	-118	2	1	0	0	0	0	tr	0	1	0	0	
Western snowberry, <i>Symphoricarpos occidentalis</i> Hook.	-8	-366	401	tr	0	0	2	tr	1	0	tr	tr	0	0	
Small soapweed, <i>Yucca glauca</i> Nutt.	181	49	-20	3	1	1	0	0	tr	tr	1	2	5	0	

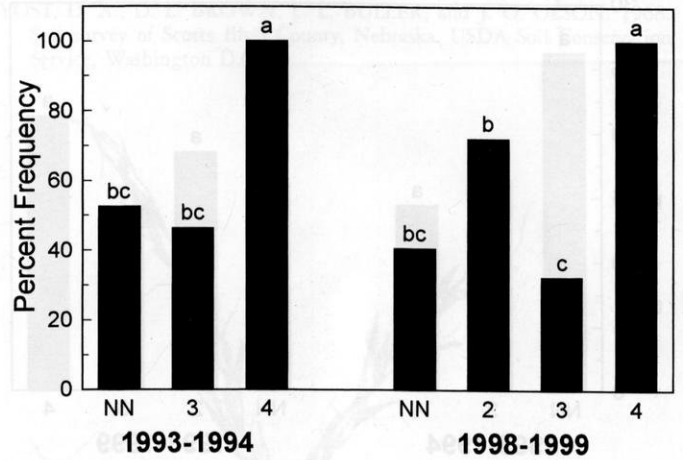
Other species occurring in $\leq 1\%$ of plots and the plots in which they were observed:

Agropyron elongatum (Host) Beauv. (3), *Agropyron trachycaulum* (Link) Malte (3), *Asparagus officinalis* L. (9), *Argemone polyanthemos* (Fedde) G. Owenby (NN, 4, 8), *Artemisia dracunculus* L. (8, 15), *Astragalus missouriensis* Nutt. (NN, NS, 8), *Atriplex canescens* (Pursh) Nutt. (3), *Camelina microcarpa* Andr. ex DC. (2, 3), *Capsella bursa-pastoris* (L.) Medic. (NS), *Cirsium ochrocentrum* A. Gray (2), *Coreopsis* spp. L. (15), *Dalea aurea* Nutt. ex Pursh (4), *Dalea candida* Michx. ex Willd. (NN, 2, 4), *Dyssodia papposa* (Vent.) Hitchc. (8), *Echinacea angustifolia* DC. (13), *Echinochloa crusgalli* (L.) Beauv. (12), *Equisetum laevigatum* A. Br. (13), *Eragrostis cilianensis* (All.) E. Mosher (8), *Eriogonum annuum* Nutt. (8, 12), *Euphorbia dendata* Michx. (2, 9), *Gaura parviflora* Dougl. (4, 15), *Gleditsia triacanthos* L. (9), *Glycyrrhiza lepidota* Pursh (NS, 2, 13), *Hordeum jubatum* L. (5), *Ipomea hederacea* Jacq. (NN), *Ipomoea leptophylla* Torr. (NS, 12, 13), *Lathyrus polymorphus* Nutt. (NN, NS, 4, 8), *Lactuca* spp. (2), *Linum rigidum* Pursh (NN, 4, 5), *Mentzelia decapetala* (Pursh) Urban & Glig (12), *Mirabilis hirsuta* (Pursh) MacM. (NN), *Muhlenbergia racemosa* (Michx.) B.S.P. (4), *Nepeta cataria* L. (3), *Oxytropis lambertii* Pursh (NN, 4), *Panicum dichotomiflorum* Michx. (NN, 4, 13), *Penstemon angustifolius* Nutt. ex Pursh (NS, 9), *Penstemon glaber* Pursh (NS, 2, 4), *Physalis hederifolia* A. Gray (15), *Plantago patagonica* Jacq. (NN), *Psoralea argophylla* Pursh (NN, 2, 4), *Psoralea esculenta* Pursh (NS, 4), *Psoralea lanceolata* Pursh (4, 5), *Rosa arkansana* Porter (NN, 5), *Rumex crispus* L. (3), *Salvia azurea* Lam. (13, 15), *Schedonnardus paniculatus* (Nutt.) Trel. (8, 13), *Senecio integerrimus* Nutt. (5), *Setaria viridis* (L.) Beauv. (2, 3, 8), *Solanum rostratum* Dun. (3, 13), *Solidago mollis* Bartl. (NN, 15), *Solidago* spp. (2), *Sorghastrum nutans* (L.) Nash (15), *Toxicodendron radicans* (L.) O. Ktze. (12), *Taraxacum officinale* Weber (2, 3), *Thelesperma fillifolium* (Hook.) A. Gray (4, 15), *Tradescantia bracteata* Small (NN, NS), *Tribulus terrestris* L. (3, 8), *Ulmus* spp. (2), *Viola nuttallii* Pursh. (NN).

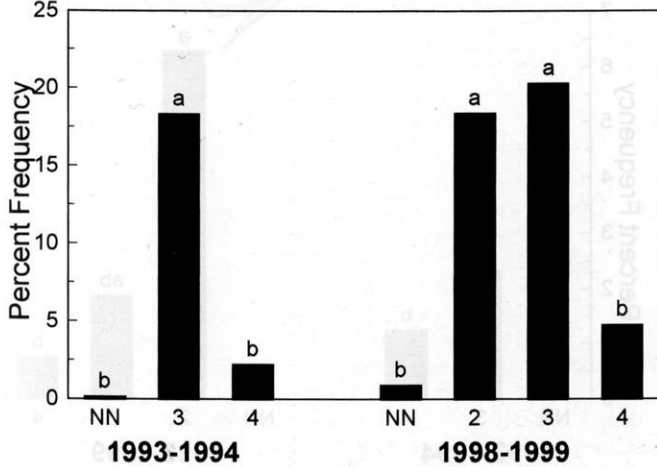
A. Native Cool-Season Grasses



B. Native Perennial Warm-Season Grasses



C. Exotic Cool-Season Grasses



D. Annual Grasses

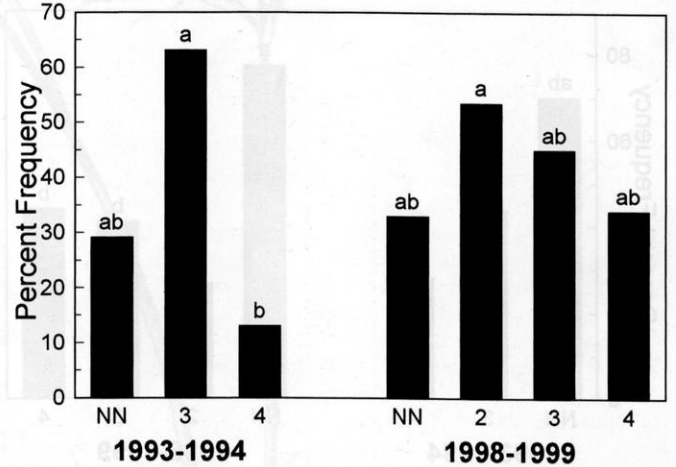


Fig. 4. Mean percent frequency by year and Restoration Group for four vegetation classes: A—native cool-season perennial grasses, B—native warm-season perennial grasses, C—exotic cool-season perennial grasses and D—annual grasses. Values with different letters were significantly different (P = 0.05).

early approaches to restoration did not produce the desired results. Although the soil was largely protected from the erosive action of wind and water (SCBL 1992), the composition of vegetation was not similar to the presettlement wheatgrass-needlegrass prairie. Presettlement vegetation should not be expected from the early restorations (1970s and 1980s) which were planted with commercial mixtures of warm-season grasses. Those reflected the seeding knowledge of grassland restoration at the time the work was done.

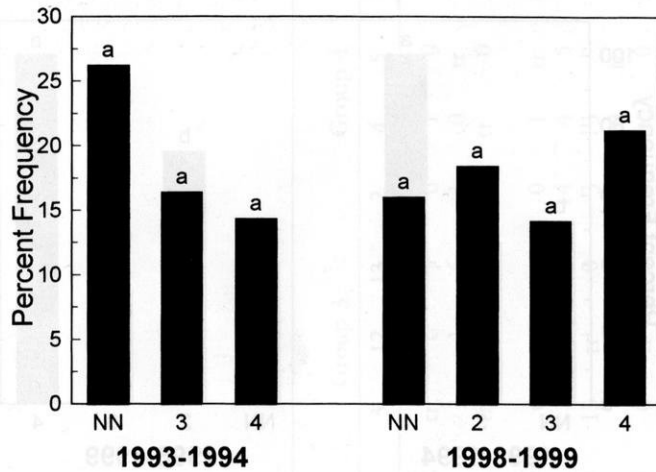
Success of later plantings conducted in the late 1980s and 1990s reflected both precipitation and species composition of the seed mixtures used. During the past 30 years, 1970, 1974, 1976, 1980, 1989 were the driest years with an average annual precipitation of 294 mm compared to the overall average annual precipitation of 415 mm. Dry conditions may have affected Restoration Sites 3 and 12 which were planted in the Fall of 1988 and 1989, respectively. In contrast, both restoration sites of Group 2 (8 and 9) were planted in years with above average precipitation (512 and 438 mm, respectively).

Other than an increase in native cool-season grasses and perennial forbs on some sites, there was little indication that the composition

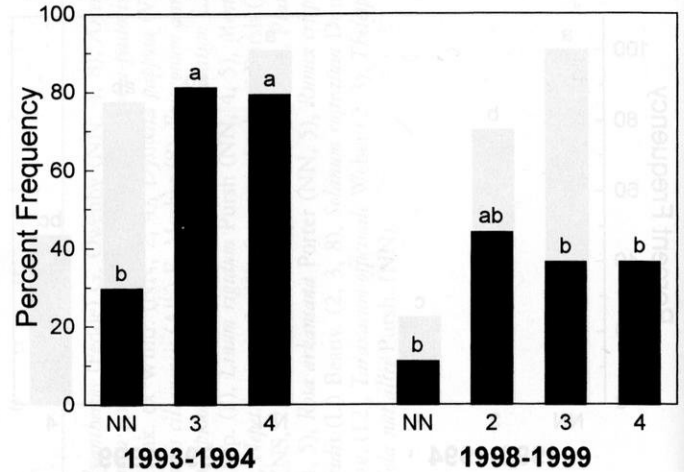
of the vegetation on Restoration Sites 2, 4, 5, 12, 13, and 15 had moved more closely to that of the native prairie sites between the initial sampling in 1993–94 and the later sampling in 1998–99. This level of sampling should detect change, but five years is a relatively short period of time for change to occur. We recommend that these sites be sampled in another five years. If significant change is not detected, it may be concluded that the vegetation is in a relatively steady state. A decision will need to be made on whether or not the vegetation composition meets restoration goals. Total restoration or partial restoration by interseeding or other methods will be options.

Restoration of Sites 8 and 9 has been highly successful. The only other Restoration Site exhibiting similar success was Site 3, which has had a decade to develop. We wish to commend National Park Service personnel involved in planning and execution of the restoration. Care was taken to develop a seeding mixture to match as closely as possible the composition of the native prairies at SCBL. The seedbeds were properly prepared, and seedings were made at the appropriate time. Post seeding management minimized erosion and competition from weeds.

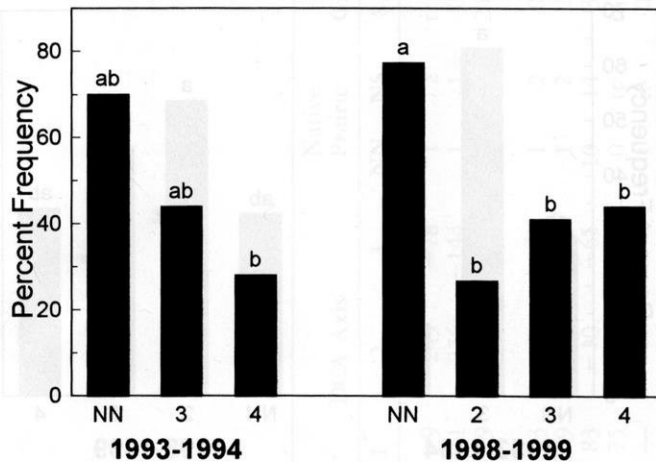
A. Native Annual Forbs



B. Exotic Annual Forbs



C. Native Perennial Forbs



D. Exotic Perennial Forbs

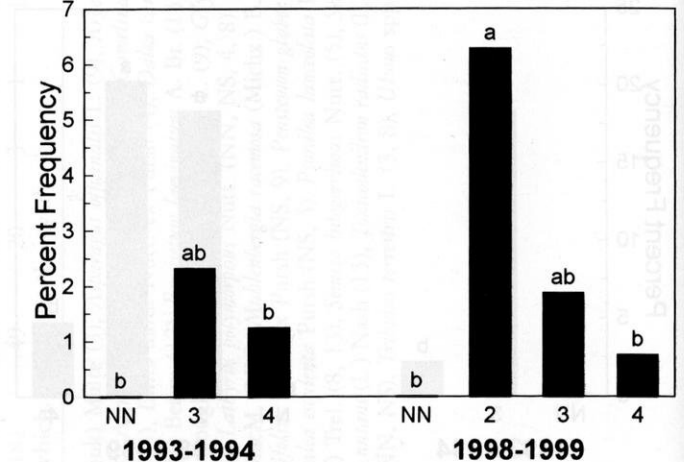


Fig. 5. Mean percent frequency by year and Restoration Group for four vegetation classes: A—native annual forbs, B—exotic annual forbs, C—native perennial forbs, and D—exotic annual forbs. Values with different letters were significantly different ($P = 0.05$).

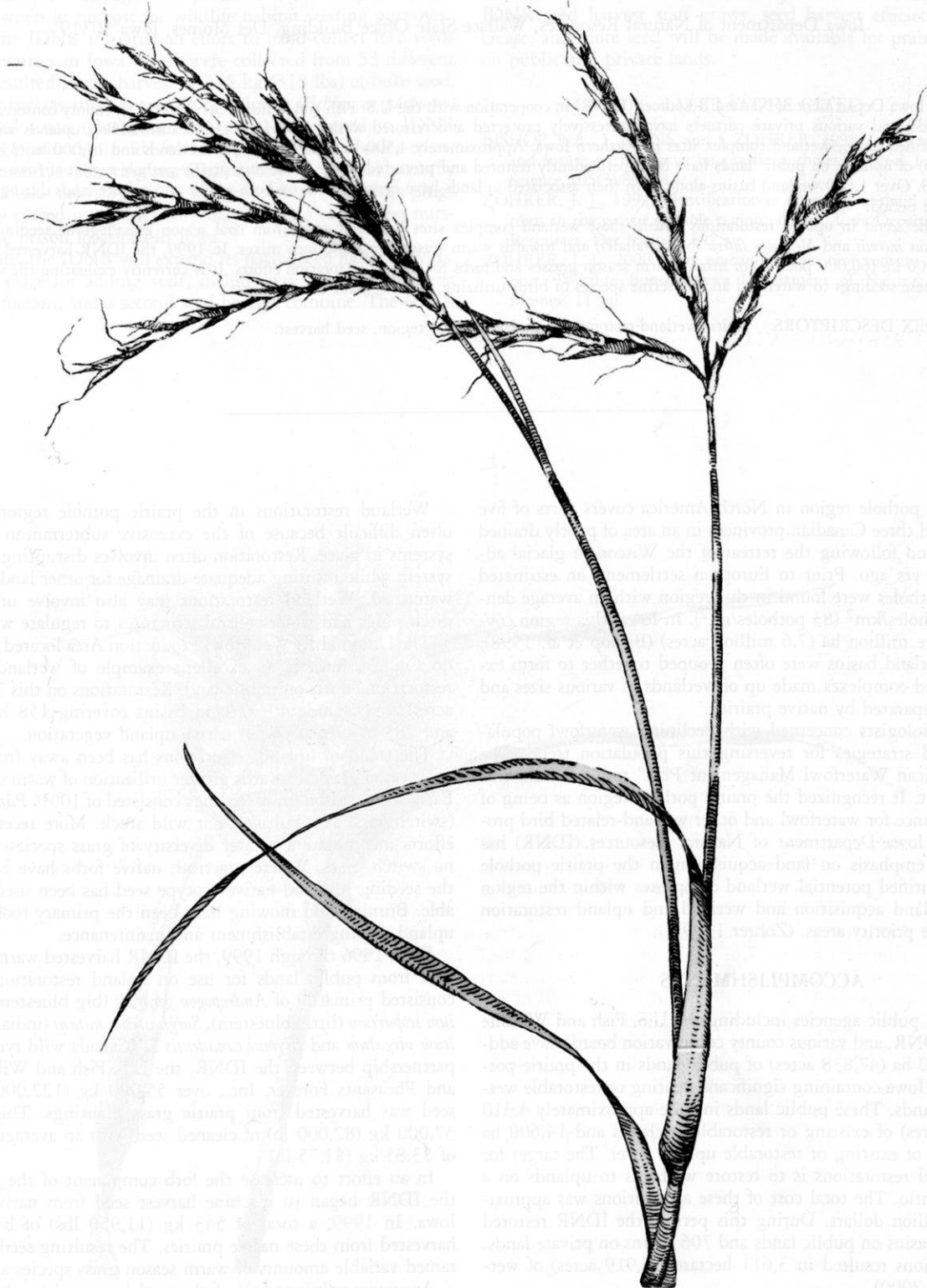
The closer affinity of the vegetation of these sites to that of the native sites is apparent in Figure 3a. This similarity is remarkable so soon after seeding Sites 8 and 9. It can be expected that some of the other native species of forbs and grasses seeded will begin to appear on these sites causing the vegetation to move, over time, more closely to that of the native sites. Due to the unavailability of seed and limited success of mechanical plugging, threadleaf sedge remains the only major species unlikely to be adequately represented in the restoration. Current work suggests that germination of threadleaf sedge is enhanced by high pretreatment temperatures, cool germination temperatures, fluctuating daily temperatures, and light (Tichota 2000). Translating these findings into successful establishment of threadleaf sedge remains to be achieved in restoration sites at SCBL.

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Prairie/Wetland Complex Restorations in the Prairie Pothole Region of Iowa

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The Iowa Department of Natural Resources (IDNR) in cooperation with the U.S. Fish and Wildlife Service (FWS), county conservation boards, and various private partners have aggressively protected and restored wetlands and associated surrounding uplands within identified prairie/wetland complex sites in northern Iowa. Approximately 4,500 ha (11,000 acres) of wetlands and 13,000 ha (33,000 acres) of uplands on public lands have been permanently restored and protected in the 35 county prairie pothole region of Iowa since 1988. Over 1,600 wetland basins along with their associated uplands have been restored on both public and private lands during this same period.

The trend in upland restorations within these wetland complex sites has been away from cool season grass/legume seedings of *Bromus inermis* and *Medicago sativa* (brome/alfalfa) and towards warm season grass and forb mixes. In 1999, the IDNR harvested over 27,000 kg (60,000 pounds) of mixed warm season grasses and forbs for upland restoration efforts. It is currently evaluating the value of these seedings to waterfowl and passerine species of birds utilizing these wetland complex sites.

INDEX DESCRIPTORS: prairie/wetland restorations, prairie pothole region, seed harvest.

The prairie pothole region in North America covers parts of five U.S. states and three Canadian provinces in an area of poorly drained soils left behind following the retreat of the Wisconsin glacial advance 12,000 yrs ago. Prior to European settlement, an estimated 25 million potholes were found in this region with an average density of 32 potholes/km² (83 potholes/mi²). In Iowa, this region covered over three million ha (7.6 million acres) (Bishop et al. 1998). Individual wetland basins were often grouped together to form extensive wetland complexes made up of wetlands of various sizes and permanency separated by native prairie.

In 1986, biologists concerned with declining waterfowl populations prepared strategies for reversing this population trend. The "North American Waterfowl Management Plan" resulted from this planning effort. It recognized the prairie pothole region as being of prime importance for waterfowl and other wetland-related bird production. The Iowa Department of Natural Resources (IDNR) has placed major emphasis on land acquisition in the prairie pothole region. It identified potential wetland complexes within the region and targeted land acquisition and wetland and upland restoration efforts in these priority areas. (Zohrer 1999).

ACCOMPLISHMENTS

Since 1988, public agencies including the U.S. Fish and Wildlife Service, the IDNR, and various county conservation boards have added over 19,000 ha (47,838 acres) of public lands in the prairie pothole region of Iowa containing significant existing or restorable wetlands and uplands. These public lands include approximately 4,310 ha (10,650 acres) of existing or restorable wetlands and 14,600 ha (36,030 acres) of existing or restorable upland cover. The target for wetland/upland restorations is to restore wetlands to uplands on a one to three ratio. The total cost of these acquisitions was approximately 43 million dollars. During this period, the IDNR restored 988 wetland basins on public lands and 706 basins on private lands. These restorations resulted in 3,611 hectares (8,919 acres) of wetlands. (Zohrer 2000).

Wetland restorations in the prairie pothole region of Iowa are often difficult because of the extensive subterranean tile drainage systems in place. Restoration often involves disrupting this drainage system while insuring adequate drainage for other landowners in the watershed. Wetland restorations may also involve utilizing dikes, ditch plugs and water control structures to regulate water flow.

The Union Hills Waterfowl Production Area located in Cerro Gordo County, Iowa is an excellent example of wetland and upland restoration efforts on public land. Restorations on this 773 ha (1,910 acres) area include 49 wetland basins covering 158 ha (390 acres) and 283 ha (700 acres) of native upland vegetation.

The trend in upland restorations has been away from the use of cool season grasses towards greater utilization of warm season species. Early warm season grass seedings consisted of 100% *Panicum virgatum* (switchgrass) as a cultivar, not wild stock. More recent restoration efforts incorporate a greater diversity of grass species with little or no switch grass. Where practical, native forbs have been added to the seeding mix and native ecotype seed has been used when available. Burning and mowing have been the primary tools utilized for upland seeding establishment and maintenance.

From 1996 through 1999, the IDNR harvested warm season grass seed from public lands for use on upland restorations. This seed consisted primarily of *Andropogon gerardii* (big bluestem), *Schizachyrium scoparium* (little bluestem), *Sorghastrum nutans* (indian grass), *Panicum virgatum* and *Elymus canadensis* L. (Canada wild rye). Through a partnership between the IDNR, the U.S. Fish and Wildlife Service, and Pheasants Forever, Inc., over 55,000 kg (122,000 lb) of bulk seed was harvested from prairie grass plantings. This resulted in 37,000 kg (82,000 lb) of cleaned seed with an average harvest cost of \$3.85/kg (\$1.75/lb).

In an effort to increase the forb component of the seeding mix, the IDNR began to machine harvest seed from native prairies in Iowa. In 1999, a total of 543 kg (11,950 lbs) of bulk seed was harvested from these native prairies. The resulting seed harvest contained variable amounts of warm season grass species and forbs.

Approximately one-half of the seed harvested by the IDNR was

used on public lands owned by the IDNR and FWS. Through a cooperative agreement, the other half was distributed by the Pheasants Forever organization to be used in a challenge program for its Iowa chapters. Chapters were given 45 kg (100 lbs) of seed if they agreed to purchase an equal amount from private local growers. All of the seed obtained through this program was then provided to private landowners at no cost for wildlife habitat seeding purposes.

In 1999, the IDNR initiated an effort to hand-collect forb seeds from native prairies in Iowa. Seeds were collected from 53 different species and resulted in the harvest of 145 kg (318 lbs) of bulk seed. Easily-grown species such as purple coneflower (*Echinacea purpurea*) and black-eyed susan (*Rudbeckia hirta*) will be planted in IDNR mixed species production fields for future harvesting. Harder to establish species such as shooting star (*Dodecatheon meadia*) and butterfly milkweed (*Asclepias tuberosa*) will be sent to growers to produce plugs which will be placed in production plots at several state forest nurseries and state prison locations in Iowa.

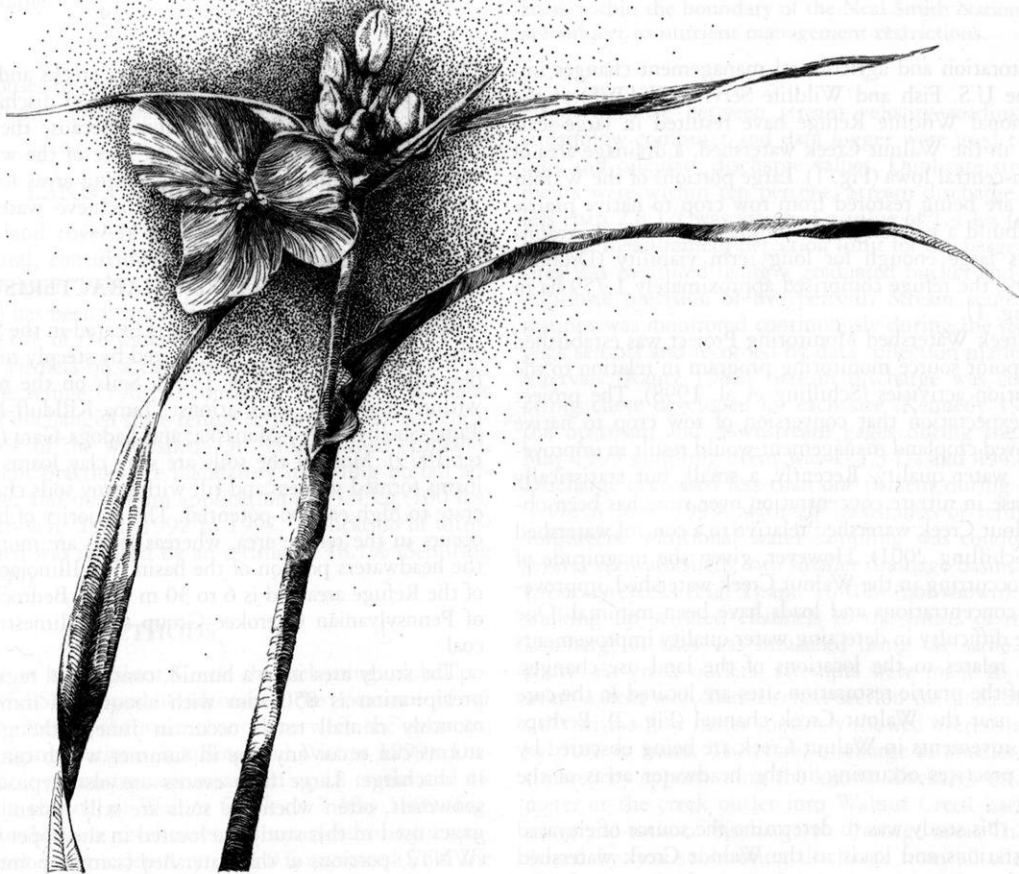
In the future, the IDNR will expand its native seed harvest efforts. Plans are in place for adding staff, including a full-time biologist and two technicians, and a second seed harvest combine. The IDNR

has also recently added field staff to work on public and private land wetland and upland restoration efforts in the Prairie Pothole Region of Iowa.

The need for native grass and forb seed, especially local-ecotype seed, is increasing as the IDNR acquires additional public lands and converts row crop fields to restored prairie. As the experience of the IDNR seed harvest staff grows, seed harvest efficiency should increase, and more seed will be made available for prairie restorations on public and private lands.

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Prairie Restoration as a BMP for Water Quality Improvement: Evidence from the Walnut Creek Watershed, Jasper County, Iowa

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Large-scale conversion of row crop to native prairie has occurred in the core of the Walnut Creek watershed but water quality improvements have been difficult to detect. We sampled 81 tributary creeks and drainage tiles over a two-day period in May 1999 during baseflow conditions to determine the source of elevated nitrate concentrations in the watershed. Nitrate concentrations ranged from <0.1 mg/L to 19 mg/L, with highest concentrations (>15 mg/L) found in headwater areas of many subwatersheds. Water draining predominantly restored prairie areas had nitrate concentration less than 1 mg/L. Nitrate loads (concentration times discharge) and loads per hectare were greatest in nine headwater drainages located in four subwatersheds. Nitrate loads exceeded 0.1 kg/day/ha in these drainage areas, which, despite constituting one third of the land area in the watershed, contributed more than 50% of the total nitrate load. Land use in these nine headwater drainages averaged more than 90% row crop. Nitrate loads in streams draining prairie or pasture were less than 0.02 kg/day/ha. A linear relationship between nitrate concentrations and percent row crop in subwatersheds was statistically significant. Results of this study have implications for placement of prairie in similar watersheds to achieve water quality improvements on a watershed scale.

INDEX DESCRIPTORS: headwater, nitrate, watershed, row crop, prairie restoration, best management practices, loads, land use, water quality.

Watershed restoration and agricultural management changes implemented by the U.S. Fish and Wildlife Service (USFWS) at the Neal Smith National Wildlife Refuge have resulted in large-scale land use changes in the Walnut Creek watershed, a drainage area of 5,222 ha in south-central Iowa (Fig. 1). Large portions of the Walnut Creek watershed are being restored from row crop to native prairie in an effort to rebuild a portion of the tallgrass prairie and savanna ecosystem that is large enough for long term viability (Drobney 1994). As of 1999, the refuge comprised approximately 1,759 ha in the watershed (Fig. 1).

The Walnut Creek Watershed Monitoring Project was established in 1995 as a nonpoint source monitoring program in relation to the watershed restoration activities (Schilling et al. 1998). The project began with the expectation that conversion of row crop to native prairie and improved cropland management would result in improvements in surface water quality. Recently, a small, but statistically significant, decrease in nitrate concentration over time has been observed in the Walnut Creek watershed relative to a control watershed (Squaw Creek) (Schilling 2001). However, given the magnitude of land use changes occurring in the Walnut Creek watershed, improvements in nitrate concentrations and loads have been minimal. One hypothesis for the difficulty in detecting water quality improvements in the watershed relates to the locations of the land use changes. Currently, most of the prairie restoration sites are located in the core of the watershed near the Walnut Creek channel (Fig. 2). Perhaps water quality improvements in Walnut Creek are being obscured by normal land use practices occurring in the headwater areas of the watershed.

The purpose of this study was to determine the source of elevated nitrate-N concentrations and loads in the Walnut Creek watershed to isolate the effects of prairie restoration on surface water quality.

Inputs of nitrate-N from 81 tributary creeks and drainage tiles were monitored during a one-time sampling of discharge rates and water quality during baseflow conditions. Because the location of refuge-owned land is concentrated in the core of the watershed, this study has important implications for choosing areas for placement of best management practices (BMPs) to achieve water quality improvements on a watershed scale.

WATERSHED CHARACTERISTICS

The Walnut Creek watershed is located in the Southern Iowa Drift Plain, a landscape area characterized by steeply rolling hills and well-developed drainage (Prior 1991). Soils on the refuge fall primarily within four soil associations: Tama-Killduff-Muscataine; Downs-Tama-Shelby; Otley-Mahaska; and Ladoga-Gara (Nestrud and Worsster 1979). Most of the soils are silty clay loams, silt loams, or clay loams formed in loess and till with many soils characterized by moderate to high erosion potential. The majority of highly-erodible land occurs in the refuge area, whereas lands are more gently sloping in the headwaters portion of the basin. Pre-Illinoian till underlies most of the Refuge area and is 6 to 30 m thick. Bedrock consists primarily of Pennsylvanian Cherokee Group shale, limestone, sandstone, and coal.

The study area is in a humid, continental region. Average annual precipitation is 850 mm with about 760 mm of snow. Highest monthly rainfall totals occur in June, although large convection storms can occur anytime in summer which can lead to rapid rises in discharge. Large flow events are also typically associated with snowmelt, often when the soils are still frozen. Two USGS stream gages used in this study are located in the upper (WNT1) and lower (WNT2) portions of the watershed (sample points 8 and 47, respectively; Fig. 1). Discharge in Walnut Creek is often very flashy, dis-

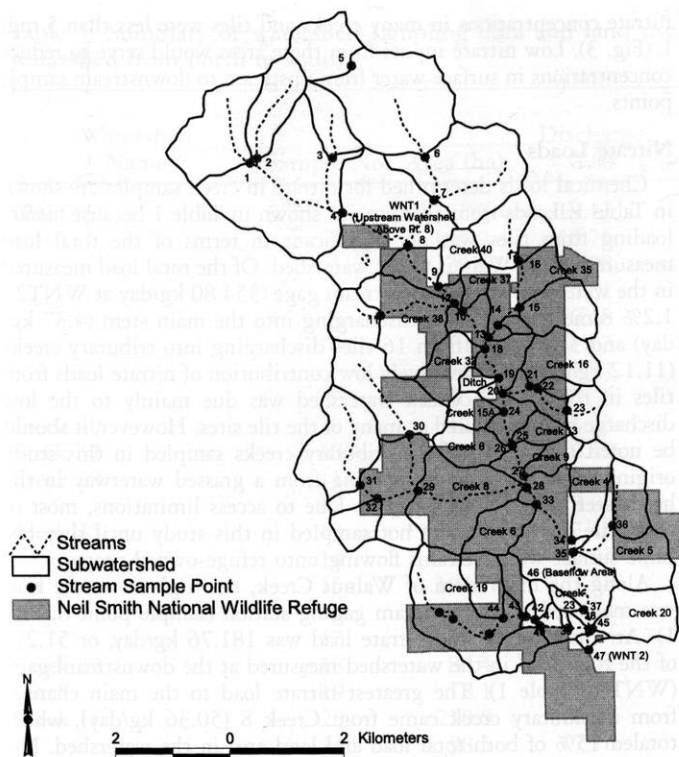


Fig. 1. Watershed boundaries and location map. Sample identification presented on Table 1.

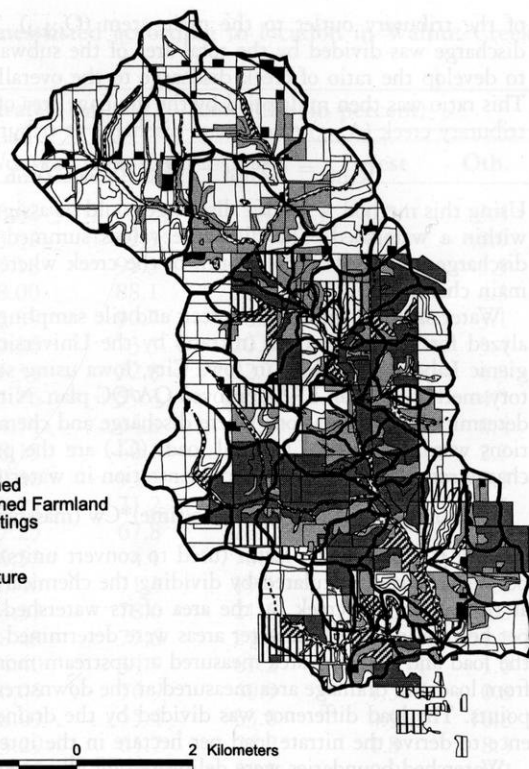


Fig. 2. Land use (1998) in the Walnut Creek watershed. Row crop areas within the boundary of the Neal Smith National Wildlife Refuge are subject to nutrient management restrictions.

playing rapid responses to precipitation. Stream discharge at WNT2 ranged from a high of 13,905 L/s to a low of 1.9 L/s (Schilling and Thompson 1999).

LAND USE CHANGES

Prior to 1992, land cover in the Walnut Creek watershed was primarily agricultural, consisting of 70% row crop and 27% grass (Schilling and Thompson 1999). From 1992 to 1999, 16.8% of the watershed (876 ha) has been converted from row crop to native prairie, with another 5.6% of the watershed (294 ha) owned by USFWS but rented to area farmers on a cash-rent basis (Fig. 2). Remaining lands owned by the refuge (590 ha) consist of forest or grass areas that have remained unchanged since refuge activities began and comprise another 11.3% of the watershed. On refuge-owned cropland, nutrient management practices are mandatory including no fall application of fertilizer and maximum application of 45.4 kg (100 lbs) of nitrogen per corn acre. From 1992 to 1997, application of nitrogen in the watershed was reduced by an estimated 18.1% (Schilling and Thompson 1999).

METHODS

Recent mapping of the Walnut Creek channel using global positioning system (GPS) equipment identified the locations of 45 creeks and 52 tiles entering the main channel between the upstream and downstream gaging stations (Schilling and Wolter 1999). Discharge rate and water chemistry was measured at 18 creeks and 19 tiles along the main channel of Walnut Creek on 7 May 1999 (Fig. 1). Surface water discharge at creek sites was measured using a standard Price AA meter set at a depth ratio of 0.6 measured from the water surface (Buchanan and Summers 1969). The maximum sepa-

ration distance between stream velocity readings was 0.3 m. A streamflow computer and data logger were used to record the readings and calculate discharge values. Duplicate streamflow measurements were within ten percent. Stream discharge determined to be less than 2.8 L/s was assigned a value of 1.4 L/s (equivalent to one-half the measurement detection limit for discharge). Discharge at tile sites was measured using a graduated bucket and stopwatch with a duplicate precision of five percent. Stream stage at USGS gaging stations was monitored continuously during the study using bubble-gage sensors and recorded by data collection platforms at 15-minute intervals (Rantz 1982). Stream discharge was computed from the rating curve developed for each site (Kennedy 1983). Discharge at the upstream and downstream gages during the midday of the 7 May 1999 sampling event was 175.3 L/s and 494.8 L/s, respectively. Discharge decreased less than one percent during the day.

On 8 May 1999, with the assistance of refuge staff and local volunteers, additional water sampling was conducted to subdivide several subwatersheds into smaller drainage basins. An additional 28 tributary creeks (Fig. 1) and 16 tiles (not shown) were identified by walking up selected channels to the limits of refuge-owned land. Discharge at tiles was measured using the same method described above. At creek outlets, attempts were made to measure discharge using a float and channel cross-section method, but comparative results with a flow meter routinely showed overestimation of discharge by 50% or more. Therefore, discharge at smaller drainages was estimated by apportioning the known discharge measured with a flow meter at the creek outlet into Walnut Creek back up the drainage using the ratio of discharge to drainage area. This ratio was determined by first subtracting discharge from all tile inputs (Q_{Tile}) in the drainage basin from the discharge total measured at the mouth

of the tributary outlet to the main stem (Q_{total}). The remaining discharge was divided by the total area of the subwatershed (A_{total}) to develop the ratio of creek discharge to the overall drainage area. This ratio was then multiplied by the drainage area of the individual tributary creek (A_{trib}) to estimate discharge at tributary creeks:

$$Q_{\text{trib}} = (Q_{\text{total}} - Q_{\text{tile}}/A_{\text{total}}) * A_{\text{trib}} \quad (1)$$

Using this method, a specific discharge could be assigned to all lands within a watershed. The discharge values summed to the known discharge measured at the mouth of the creek where it entered the main channel.

Water samples collected at creek and tile sampling sites were analyzed for nitrate-nitrogen (nitrate) by the University of Iowa Hygienic Laboratory (UHL) in Iowa City, Iowa using standard laboratory methods and an EPA-approved QA/QC plan. Nitrate loads were determined at all locations where discharge and chemical concentrations were measured. Chemical loads (CL) are the products of discharge rate (Q) and chemical concentration in water (Cw) where

$$CL \text{ (mass/time)} = Q \text{ (volume/time)} * Cw \text{ (mass/volume)} * CF \quad (2)$$

and CF is a conversion factor (used to convert units). Nitrate loads per hectare were calculated by dividing the chemical load measured at the outlet of a creek by the area of its watershed. Nitrate loads per hectare in some headwater areas were determined by subtracting the load and drainage area measured at upstream monitoring points from load and drainage area measured at the downstream monitoring points. The load difference was divided by the drainage area difference to derive the nitrate load per hectare in the intermediate area.

Watershed boundaries were delineated for all creeks sampled during the study and entered into a geographic information system (GIS) using ArcView (Environmental Systems Research Institute, Inc. 1998). Land use percentages were determined for each watershed by intersecting the creek watershed boundaries with 1998 land cover data (Schilling and Thompson 1999) (Table 1).

RESULTS

Nitrate Concentrations

Nitrate concentrations from tributary creeks and tiles ranged from less than the detection limit (<0.1 mg/L) in several samples to 19 mg/L in a tributary creek in the Creek 8 watershed (Fig. 3). Concentrations were greater than 15 mg/L in the headwater areas of many subwatersheds (Fig. 3). In eight creek samples collected above the WNT1 gaging station, nitrate concentrations ranged from 12 to 17 mg/L. In many cases, nitrate concentrations that started elevated in surface water samples collected at headwater areas remained high as the water flowed through the subwatershed and discharged into the Walnut Creek channel (Fig. 3).

Some decrease in nitrate concentration was observed between upstream and downstream samples in several watersheds (Fig. 3). In the entire Walnut Creek watershed, nitrate concentrations decreased from 12 mg/L at the upstream stream gage (WNT1; sample point 8) to 8.3 mg/L at the downstream gage (WNT2; sample point 47). Decreasing nitrate concentrations with stream flow may occur as a result of nitrogen assimilation (Isenhardt and Crumpton 1989), denitrification in stream sediments (Hill 1981), and periphyton (Duff et al. 1984). In some cases, reduction of nitrate concentrations from upstream to downstream sample sites may be due to dilution from low nitrate inputs. In areas draining restored prairie areas, nitrate concentrations were substantially less in surface water compared to areas draining agricultural lands. In three watersheds draining mostly restored prairie areas (Creeks 6, 9 and 13), nitrate concentrations were less than 1 mg/L (Table 1). Along the main stem of Walnut Creek where riparian land use is dominated by prairie and forest,

nitrate concentrations in many creeks and tiles were less than 5 mg/L (Fig. 3). Low nitrate inputs from these areas would serve to reduce concentrations in surface water from upstream to downstream sample points.

Nitrate Loads

Chemical loads determined for nitrate in creek samples are shown in Table 1. Loads from tiles are not shown in Table 1 because nitrate loading from tiles was not significant in terms of the total load measured in the Walnut Creek watershed. Of the total load measured in the watershed at the downstream gage (354.80 kg/day at WNT2), 1.2% came from 19 tiles discharging into the main stem (4.37 kg/day) and 3.1% came from 16 tiles discharging into tributary creeks (11.12 kg/day). The relatively low contribution of nitrate loads from tiles in the Walnut Creek watershed was due mainly to the low discharge rates measured at many of the tile sites. However, it should be noted that many of the tributary creeks sampled in this study originated as tile flow discharging from a grassed waterway in the headwater areas of many basins. Due to access limitations, most of these tile discharges were not sampled in this study until they became surface water streams flowing onto refuge-owned property.

Along the main stem of Walnut Creek, the highest nitrate load was measured at the upstream gaging station (sample point 8; Fig. 1). At this location, the nitrate load was 181.76 kg/day, or 51.2% of the total load in the watershed measured at the downstream gage (WNT2) (Table 1). The greatest nitrate load to the main channel from a tributary creek came from Creek 8 (50.36 kg/day), which totaled 15% of both total load and land area in the watershed. Nitrate loads from four tributary creeks (Creeks 8, 38, 35 and 19; Fig. 1) totaled 71.5% of the total load entering the main channel between the two gaging stations. All told, contributions of nitrate loads from 18 tributary creeks (not including WNT1) totaled 165.59 kg/day, or 46.7% of the watershed load.

In many areas, sources of nitrate loading in major tributary creeks were traced to headwater areas. In the WNT1 subwatershed, four small headwater basins (samples 1, 2, 3 and 5; Fig. 1) accounted for 35.3% of the total load measured at WNT1. In the Creek 8 watershed, the nitrate load contribution from headwater areas was even more pronounced. Of the total nitrate load measured at the mouth of Creek 8, 93% of the load originated above the confluence of two tributary streams (sample point 29; Fig. 1). The lower portion of the Creek 8 watershed, containing most of the restored prairie, contributed only 3.28 kg/day, or 7% of the total load in the watershed. Further up the Creek 8 watershed, 43% (21.85 kg/day) of the nitrate load came from the tributary measured at sample 31, and 36% (16.22 kg/day) came from the tributary measured at sample 30 (Table 1). In the entire Creek 8 subwatershed, 76% of the nitrate load was coming from 46% of the land area. This trend was demonstrated in other watersheds as well. In the Creek 16 subwatershed, 66% of the nitrate load was coming from the headwater portion of the watershed sampled at stop 33, contributing only 23% of the land area. In the Creek 38 and 19 subwatersheds, more than 50% of the total load was coming from headwater drainages.

Many water samples were collected from tributary drainages at locations where surface water entered refuge-owned property from upstream areas. As noted in Figure 2, much of the refuge is located in the core of the Walnut Creek watershed. Based on the loading data, 84% of the nitrate load in Walnut Creek was coming from non-refuge land, which comprised approximately 66% of the total land area of the watershed.

Nitrate Loading Per Hectare

In an effort to normalize the nitrate loads to an equal land area, nitrate loads were divided by the number of hectares in each drainage

Table 1. Summary of watershed sampling data and land use. Watershed names listed according to location in Walnut Creek watershed from north to south.

Watershed Name	Sample No.	Area (ha)	Discharge (L/s)	Nitrate Conc (mg/L)	Nitrate Load (kg/day)	Land Use (in percent)			
						Row Crop	Grass	Forest	Oth.
WNT1	1	181.2	18.12	17.0	26.62	93.2	3.4	0.0	3.4
	2	105.9	10.76	14.0	13.02	92.3	1.8	0.0	5.9
	3	70.6	7.08	15.0	9.18	95.3	1.2	0.0	3.5
	4	752.5	75.61	15.0	98.00	88.1	12.3	0.0	4.3
	5	104.1	10.48	17.0	15.39	90.7	6.2	0.0	3.1
	6	414.7	41.63	14.0	50.36	73.5	20.8	2.3	3.4
	7	676.5	67.97	13.0	76.34	72.8	22.7	0.2	4.3
	8	1746.6	175.30	12.0	181.76	59.3	35.7	0.3	4.7
Creek 40	9	47.9	6.23	8.8	4.74	34.8	62.5	2.2	0.4
Creek 37	10	31.3	0.40	4.5	0.15	60.1	37.2	0.0	2.7
Creek 38	11	66.0	7.45	16.0	10.30	93.6	4.1	0.0	2.3
	12	250.4	28.89	12.0	29.95	71.2	14.2	9.2	5.5
Creek 35	13	349.9	37.10	8.5	27.25	67.8	26.0	3.6	2.7
	14	10.4	0.74	8.3	0.53	4.1	78.5	17.4	0.0
	15	103.7	7.48	9.9	6.40	71.3	19.1	9.7	0.0
	16	33.7	2.44	16.0	3.37	78.6	21.2	0.0	0.2
	17	90.9	6.54	15.0	8.48	77.6	21.0	0.0	1.5
Creek 32	18	80.4	8.21	6.2	4.40	34.9	61.2	2.9	1.0
Ditch	19	18.1	0.48	1.2	0.05	56.9	40.9	1.5	0.8
Creek 16	20	210.0	16.43	5.7	8.09	55.4	33.0	0.9	10.8
	21	98.5	7.76	4.9	3.29	65.7	24.2	1.8	8.3
	22	18.1	1.42	5.1	0.62	66.8	32.5	0.0	0.7
	23	49.2	3.88	16.0	5.36	62.5	32.6	0.0	5.0
Creek 15A	24	44.1	2.83	6.9	1.69	42.1	57.7	0.0	0.2
Creek 13	25	36.3	1.98	0.4	0.07	10.4	89.4	0.0	0.2
Creek 12	26	70.0	6.23	5.1	2.75	35.3	58.5	1.4	4.8
Creek 9	27	39.2	2.83	0.8	0.20	24.5	73.1	2.4	0.0
Creek 8	28	806.1	59.47	9.8	50.36	55.1	36.8	2.8	5.3
	29	601.3	41.91	13.0	47.08	40.4	52.9	0.0	6.7
	30	194.6	14.44	13.0	16.22	75.1	20.7	0.0	4.2
	31	178.8	13.31	19.0	21.85	91.3	0.9	3.7	4.0
	32	53.2	3.96	12.0	4.11	77.2	19.1	2.2	1.4
Creek 6	33	79.2	1.42	<0.1	0.00	6.2	81.9	2.4	9.5
Creek 4	34	95.6	9.74	13.1	11.02	90.0	4.0	0.0	6.0
Creek 5	35	212.5	16.99	4.3	6.31	37.6	56.7	0.4	5.3
	36	75.0	11.47	7.2	7.14	40.6	57.3	0.0	2.1
Creek 23	37	15.6	1.42	9.8	1.20	23.1	55.8	20.9	0.1
Creek 19	38	451.0	39.65	6.1	20.90	55.4	21.4	15.2	8.0
	39	2.6	0.28	5.6	0.14	74.0	12.6	0.0	13.4
	40	46.7	3.88	3.2	1.07	9.9	52.9	36.4	0.8
	41	17.9	1.50	12.0	1.56	62.4	0.0	33.1	4.5
	42	36.3	3.00	3.8	0.99	29.8	34.4	34.5	1.3
	43	233.3	19.37	6.8	11.38	68.6	10.1	12.8	8.6
	44	70.0	5.81	4.5	2.26	60.0	33.7	0.0	6.3
Creek 20	45	111.5	5.66	13.0	6.36	81.9	16.6	1.5	0.1
Baseflow area	46	527.2	(1)	(1)	(1)	31.5	46.6	11.2	10.7
WNT2 (entire watershed)	47	5220.8	494.8	8.3	354.80	60.2	29.1	1.2	8.5

(1) Baseflow nitrate concentration and load estimated (see text for explanation).

area. Of the subwatersheds draining to the main stem of Walnut Creek, greatest nitrate loads per ha were identified in the WNT1 subbasin and tributary creeks 38 and 40 (Fig. 4). Each of these subwatersheds indicated nitrate loads per ha greater than approximately 0.09 kg/day/ha. In contrast, five subwatersheds showed nitrate loads per ha less than 0.025 kg/day/ha (Fig. 4). Among these

watersheds, Creeks 6, 9 and 13 are located in portions of the watershed dominated by restored prairie (Fig. 2). In the Creek 8 watershed, even though a large percentage of land has been restored to prairie (23.2%, Schilling and Thompson 1999), nitrate load per ha, as measured at the mouth of the creek, remained high (0.062 kg/day/ha).

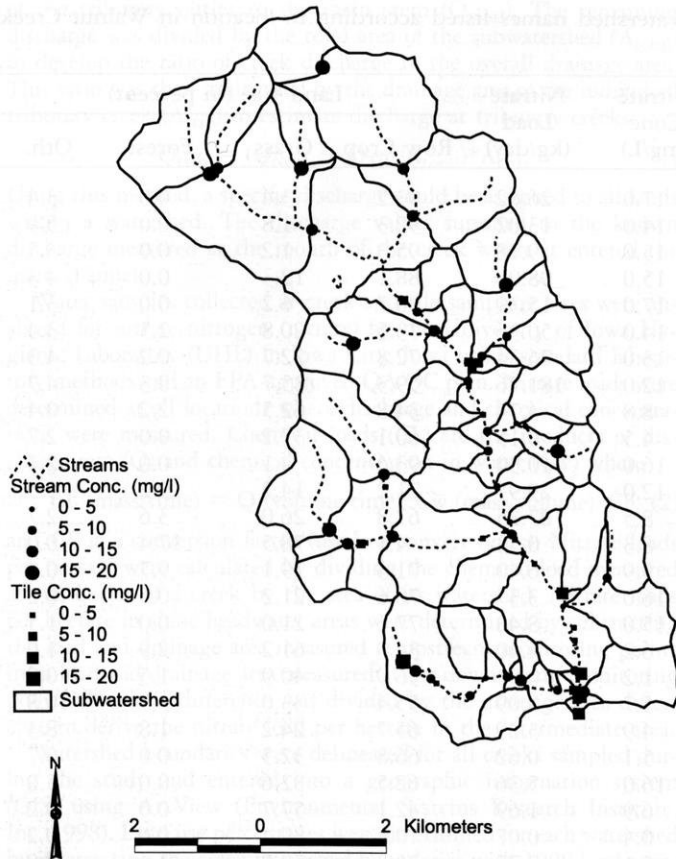


Fig. 3. Geographic distribution of nitrate concentrations in surface water and tile samples. Surface water sample points identified in Figure 1.

Areas of the watershed not included in a specific drainage basin were considered the areas contributing to baseflow discharge to the main stem (Fig. 4). Although baseflow loads were not directly measured, a mass balance approach to estimate baseflow loads showed nitrate loads were minor compared to surface water inputs (Schilling and Wolter 2001). The baseflow area includes a large percentage of restored prairie area and abundant non-prairie, riparian vegetation. Therefore, it is reasonable to assume that the baseflow area of the watershed contributes less than 0.025 kg/day/ha (Fig. 4).

Subdividing nitrate loads in subwatersheds into smaller tributary drainages indicated highest nitrate loads per ha were located in various headwater areas (Fig. 5). Of the 45 subwatersheds sampled in this study, nine drainages (20 percent) showed nitrate loads per ha greater than approximately 0.10 kg/day/ha, six of which are located in the WNT1 subwatershed (Fig. 5). Nitrate loads per ha ranged from 0.097 to 0.143 kg/day/ha in these six drainage areas (Table 1). Elsewhere, high nitrate loading per ha was evident in headwater basins in Creek 8 and Creek 38 and the entire Creek 4 watershed (Fig. 5).

Nitrate loads per ha determined by sampling at the outlet of a tributary creek, as shown in Figure 4, did not necessarily reflect the source of nitrate loading in the watershed. In the Creek 8 watershed, nitrate loading per ha was substantially less in the lower portion of the watershed compared to headwater areas (Fig. 5). The lower portion consists nearly entirely of restored prairie (Fig. 2), where the nitrate load per ha (0.016 kg/day/ha) was similar to other restored prairie watersheds (i.e., Creek 6). The nitrate load per ha of the entire

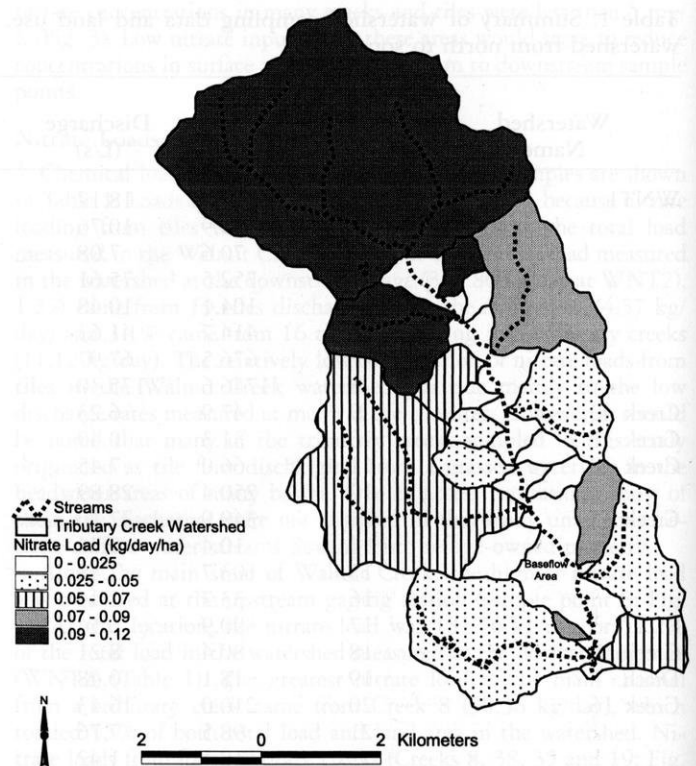


Fig. 4. Nitrate loads per hectare in watersheds.

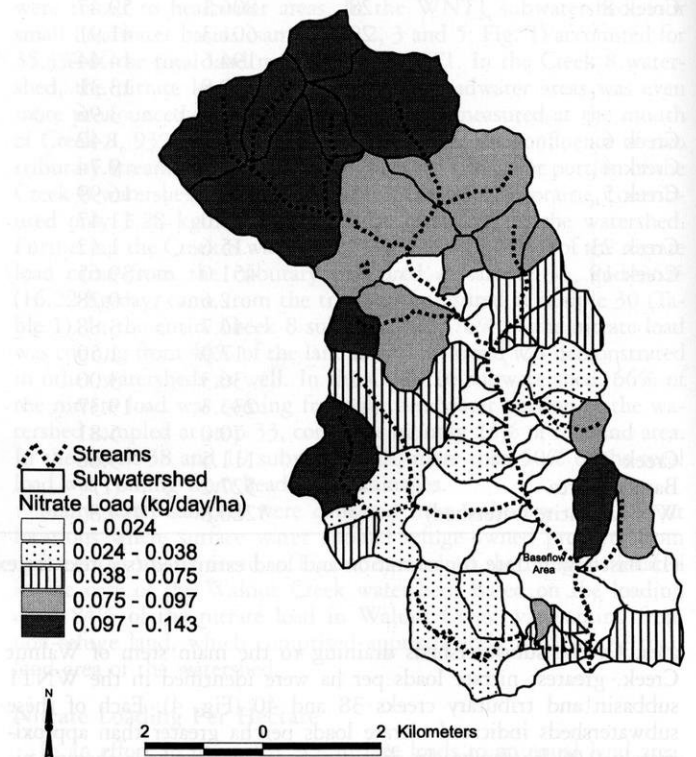


Fig. 5. Nitrate loads per hectare in subwatershed areas.

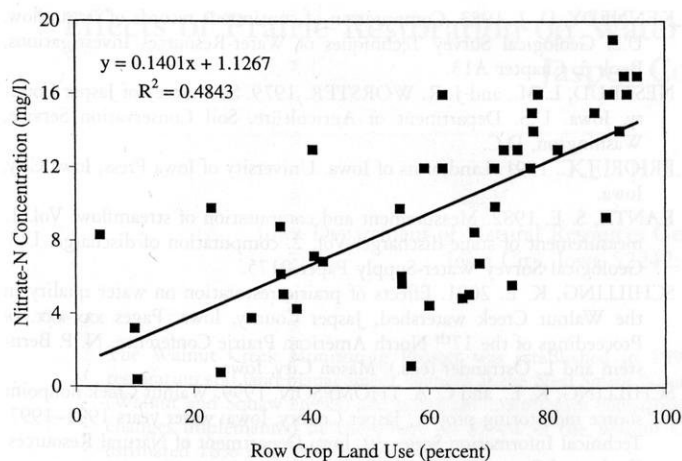


Fig. 6. Relationship of nitrate concentrations and percentage of row crop in Walnut Creek watersheds.

watershed (0.062 kg/day/ha), as measured at the mouth of Creek 8, reflected primarily contributions from headwater areas. Similar to Creek 8 watershed, reduced nitrate loads per ha were also noted in the lower portions of WNT1 and Creek 5 watersheds. In the lower WNT1 watershed, much of the riparian zone of Walnut Creek consists of grass and pasture unlike the upper portion of the watershed dominated by row crop (Fig. 2). The nitrate loading data suggest that caution is needed when characterizing water quality on a watershed scale by simply sampling at the mouth of the watershed. The water sample collected at the watershed mouth integrates contributions from all areas within the watershed and may not reflect the variability of nutrient loading within the basin.

Relationship to Land Use

Headwater areas in the Walnut Creek watershed are dominated by row crop agriculture because these lands consist of relatively flat upland divides. In the pre-Illinoian glacial landscape found in southern Iowa, much of the land is in hillslope that is less well-suited for intensive row crop production. Therefore, row crop production is intensified on gentle-sloping watershed divides. Tributary drainages often originate in these divides by tile or creek discharge from row crop fields and consequently show elevated nitrate concentrations and loads. On a load per unit area basis, the nine highest nitrate loads were found in surface water draining headwater areas where land use averaged more than 90% row crop. These nine watersheds comprised 32% of the land area in the Walnut Creek watershed but contributed 54% of the total nitrate load. In the Creek 8 subwatershed, 84% of the nitrate load was coming from three headwater basins containing more than 70% row crop. These three subwatersheds comprised only 53% of the land area in the Creek 8 basin.

Although some scatter exists in the data, regression analysis indicates the relationship between row crop land use and nitrate concentrations in the Walnut Creek watershed is highly significant ($P < 0.05$) (Fig. 6). A similarly strong relationship ($P < 0.05$) exists between row crop land use and nitrate loads. The y-intercept of the regression line suggests that nitrate concentrations should be less than one if there were no row crop. This would appear to be realistic considering that subwatersheds consisting nearly entirely of restored prairie showed nitrate concentrations less than one mg/L.

Although much of the refuge-owned cropland is scattered throughout the watershed, the small drainage basin above sample 22 (Fig. 1) contained a large percentage (Fig. 2). In this one watershed,

nitrate loads per acre (0.034 kg/day/ha) were less than those observed in watersheds containing a similar percentage of row cropland (Fig. 6). Although just one point, this suggests that nitrogen restrictions on refuge-owned land may contribute to less nitrate lost per acre.

DISCUSSION

Data from this study suggest that prairie restoration is having an effect on nitrate concentrations and loads in the Walnut Creek watershed. Surface water draining watersheds dominated by restored prairie showed nitrate concentrations less than 1 mg/L and loads per unit area less than 0.02 kg/day/ha. These values were substantially less than nitrate concentrations and loads per unit area measured in surface water draining row crop areas (>10 mg/L and >0.1 kg/day/ha, respectively). However, the effects of prairie restoration on water quality have been difficult to distinguish at the watershed scale due to the contribution from headwater areas dominated by row crop.

Results suggest that, in the Walnut Creek watershed, placement of BMPs may be more appropriate for headwater areas rather than in the core of the watershed to achieve water quality improvements on a watershed scale. Implementation of appropriate BMPs in headwater areas could result in larger improvements in overall watershed water quality. For example, if BMPs could reduce nitrate loading rates in the WNT1 subwatershed by 25% (from 181 kg/day to 136 kg/day), nitrate loads in the entire watershed would be reduced by 12.8%. If this occurred, mean nitrate concentrations measured at the watershed outlet would be reduced from 8.3 to 7.2 mg/L, an improvement of approximately 1 mg/L. Targeting BMPs in the Creek 8 subwatershed would focus on reducing loads in the two main headwater drainages. If nitrate loads in the two drainages above samples 30 and 31 were reduced by 50%, the load measured at the mouth of Creek 8 where it discharges into Walnut Creek would be reduced by 38%. The nitrate load in the entire watershed subsequently would be reduced by 5.4%. Nitrate concentrations measured at the mouth of Creek 8 could then be reduced from 9.8 mg/L to 6.1 mg/L. This would represent an improvement that could be readily detected in a watershed monitoring program.

BMPs for reduction of nitrate concentrations in the Walnut Creek watershed could involve reduction of ammonia applications in headwater areas or constructed wetlands at select tile outlets. In one small drainage area where effects of reduced nitrogen application could be monitored (sample 22), mandated reduction of nitrogen application rates by one-third suggests nitrate concentrations in surface water could be substantially reduced. According to the relationship between row crop percentage and nitrate concentrations developed for the watershed, the percentage of row crop in the subwatershed (66.8%) should have resulted in nitrate concentrations in surface water of about 10.4 mg/L. Instead, the nitrate concentration measured in surface water was 5.1 mg/L, a hypothetical reduction in concentration of more than 50%.

Although it is recognized that restoring row crop fields to native prairie is not a practical solution for large watersheds, this study demonstrates that prairie restoration can play a role in improving water quality. At the subwatershed scale, prairie restoration has the ability to measurably improve nitrate concentrations and loads in surface water. In larger watersheds, prairie restoration may serve more to dilute high concentrations and loads emanating from row crop fields by contributing baseflow water low in nitrate. Placement of BMPs in watersheds should consider a similar sampling effort of measuring water concentration and discharge (loads) at the subwatershed level. Areas showing highest loads per acre could then be targeted with specific BMPs, such as prairie, to have greatest potential for improving water quality on a watershed scale.

ACKNOWLEDGEMENTS

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Effects of Prairie Restoration on Water Quality in the Walnut Creek Watershed, Jasper County, Iowa

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The Walnut Creek Monitoring Project was established in 1995 as a nonpoint source monitoring program in relation to prairie restoration and land management changes at the Neal Smith National Wildlife Refuge. The project utilizes a paired watershed approach (Walnut and Squaw creeks) and upstream/downstream comparisons for analysis and tracking of trends. From 1992 to 1997, land use changes implemented by the refuge on 22.4% of the Walnut Creek watershed have reduced nitrogen and pesticide applications an estimated 18% and 28%, respectively.

Atrazine has been the most frequently detected pesticide in surface water (80%) in both Walnut and Squaw creek watersheds. No significant differences have been noted in atrazine concentrations and loads. A t-test showed a significant difference between mean nitrate concentrations in the Walnut and Squaw creek data sets (8.37 mg/l and 9.36 mg/l, respectively). Regression analyses indicated a decrease in nitrate concentrations over time in the Walnut Creek watershed in relation to the Squaw Creek watershed and between upstream and downstream samples collected in Walnut Creek. Increasing divergence between treatment and control samples can be traced to increasing nitrate concentrations over time at both Squaw Creek and upstream Walnut Creek sampling sites which were not observed at the Walnut Creek watershed outlet. Results from the Walnut Creek Monitoring Project demonstrate the need to follow projects for several years to begin to see water quality improvements resulting from prairie restoration.

INDEX DESCRIPTORS: Nonpoint source pollution, water quality, Neal Smith National Wildlife Refuge, nitrate, atrazine.

In Iowa, nonpoint source (NPS) pollution is a major cause of impairment to water quality. Recent assessments show that agricultural land use is the source of diffuse, NPS pollution affecting approximately 96% of Iowa's streams and the majority of lakes and wetlands (Agena et al. 1990). In the southern Iowa region, more than 30 lakes and wetlands, and several river or stream segments have been listed as impaired on the State of Iowa's 1998 303(d) list due to excessive sediment, nutrients, pesticides and animal waste runoff.

Numerous programs employing a variety of best management practices (BMPs) have been implemented in Iowa to mitigate NPS pollution from agriculture. However, monitoring NPS water-quality improvements resulting from BMPs has rarely been done because it is not an easy task. NPS pollution results from runoff across a landscape with varied land-management practices. The resultant NPS impacts measured in perennial streams are typically a mix of effects from many different parcels of land and many different components of management, integrated over many time scales. Hence, it is difficult to document the relationship between improvements in water quality and changes in management practices on a watershed scale. Many projects implemented under Section 319 of the Clean Water Act have had little or no monitoring associated with them. Water quality improvements are generally assumed rather than measured, or estimated using field-scale or watershed models.

The Walnut Creek Watershed Restoration and Water-Quality Monitoring Project is providing a valuable opportunity to measure quantitatively, on a watershed scale, water quality improvements resulting from large-scale land use changes. The Walnut Creek Watershed Monitoring Project was established in 1995 as a NPS monitoring program in conjunction with watershed habitat restoration and agricultural management changes implemented by the U.S. Fish

and Wildlife Service (USFWS) at the Neal Smith National Wildlife Refuge and Prairie Learning Center (Refuge) in Jasper County, Iowa (Fig. 1). A large portion of the Walnut Creek watershed is being restored from row crop agriculture to native prairie and/or savanna. Riparian zones and wetlands are being restored in context, with riparian zones grading from prairie waterways, to savanna, to timbered stream borders (Drobney 1994, Schilling et al. 1998). Although it is not expected that large-scale prairie restoration will ever be used as an NPS management practice, the magnitude of the land use changes within the Walnut Creek watershed is large compared to other watershed projects. This project is forming a baseline against which to set expectations for other watershed improvement projects and establishing the amount and location of non-agricultural land that might be placed in watersheds to reach a given water quality objective.

The monitoring project utilizes a paired-watershed approach (Walnut and Squaw creeks) as well as upstream/downstream comparisons (Walnut Creek only) for analysis and tracking of trends (Fig. 1). The Walnut Creek watershed is paired with the Squaw Creek watershed, which shares a common basin divide with Walnut Creek, to minimize precipitation variation. Several subbasins are also being monitored in each watershed to allow comparisons of differential implementation over time and for analyzing their incremental contributions to the overall watershed response. Basin characteristics of the Walnut and Squaw Creek watersheds are similar and make them well suited for a paired watershed design. Walnut Creek drains 5,222 ha and discharges into the Des Moines River at the upper end of the Red Rock Reservoir. The Squaw Creek drains 4,744 ha above its junction with the Skunk River. Both watersheds are located on the Southern Iowa Drift Plain, a pre-Illinoian glacial landscape charac-

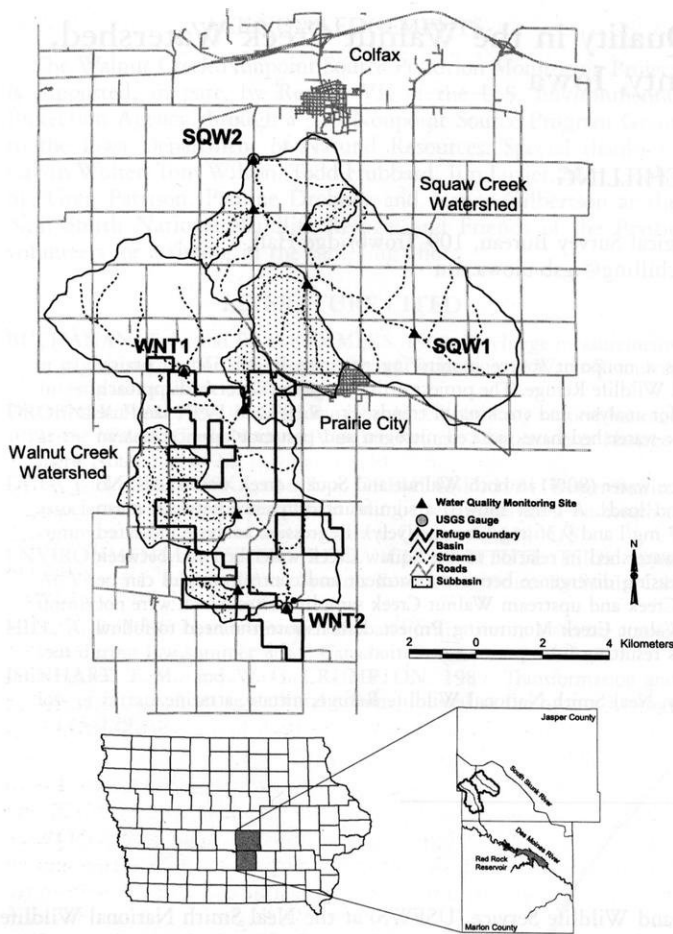


Fig. 1. Location map of the Walnut Creek and Squaw Creek watersheds, central Iowa.

terized by steeply rolling hills and well-developed drainage (Prior 1991).

Land restoration activities began in the Walnut Creek watershed in 1992, and by 1993, full scale restoration and improved agricultural management were implemented on Refuge-owned lands. Monitoring in the Walnut Creek and Squaw Creek watersheds began on a limited basis in 1994, and full-scale monitoring commenced in 1995. From project startup, five basic components have comprised the project: 1) tracking of land cover and land management changes within the basins, 2) stream gauging for discharge and suspended sediment at two locations on Walnut Creek and one on Squaw Creek, 3) surface water quality monitoring of Walnut and Squaw creeks, 4) biomonitoring for aquatic macroinvertebrates and fish in Walnut and Squaw creeks, and 5) groundwater quality and hydrologic monitoring (Fig. 1). In this paper, land use and surface water quality monitoring results for nitrogen and pesticides are reported for the main stem sampling sites (1995 to 1999). Additional data regarding other monitoring components can be found in Schilling and Thompson (1999) and Schilling (2000).

METHODS

Land use practices for both watersheds have been tracked on a yearly basis throughout the course of the project using a combination of plat maps, Natural Resources Conservation Service (NRCS) crop

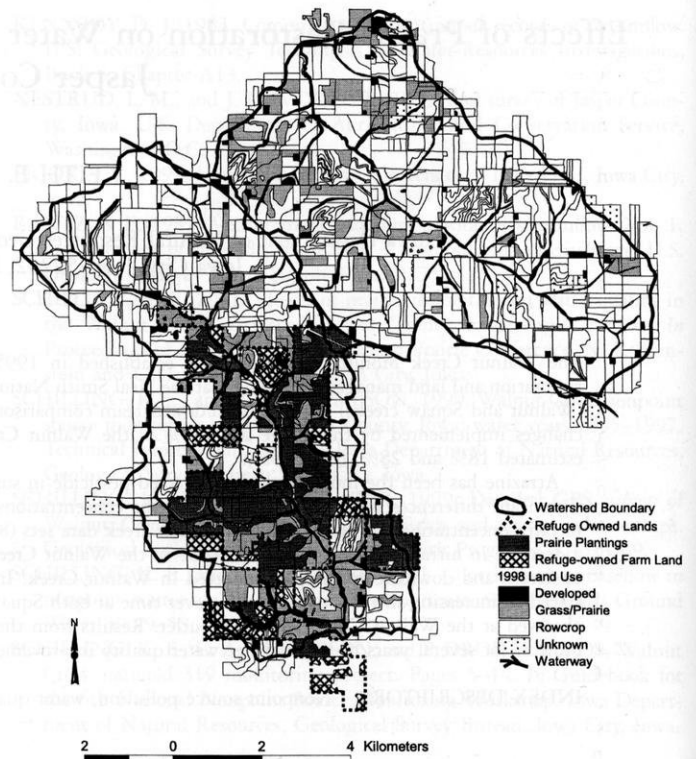


Fig. 2. Land cover in the Walnut Creek and Squaw Creek watersheds for 1999.

data, aerial photographs and field surveys. USFWS personnel have tracked prairie planting areas and locations of rental ground in the Walnut Creek watershed. Land cover data were entered into a Geographic Information System (GIS) using ArcView and coupled with the water quality, flow, and sediment data for analysis. USGS gaging stations are located at the bottom of each watershed and an additional gage is located at the upper end of the Walnut Creek watershed where the majority of refuge land begins. Surface-water chemistry is monitored weekly to monthly at ten sites in the Walnut and Squaw creek basins and analyzed for anions, pesticides (in season), fecal coliform and field parameters (dissolved oxygen, turbidity, alkalinity, conductivity, and temperature). Laboratory analyses are performed by The University of Iowa Hygienic Laboratory (UHL) using standard methods and an EPA-approved QA/QC plan. Statistical comparisons between data sets (t-tests, regression) were performed using a spreadsheet program package (Excel 7.0) according to the guidelines of Grabow et al. (1998).

RESULTS

Land Use Tracking

In 1992, land use in the Walnut and Squaw creek watersheds consisted of 70% row crop and 27% grass (Schilling and Thompson 1999). From 1992 to 1998, 876 ha (16.8%) of the Walnut Creek watershed have been converted from row crop to native prairie (Fig. 2). During this same time period, land use in the Squaw Creek watershed has remained essentially unchanged. In addition to the land conversions, 294 ha of refuge-owned lands in the Walnut Creek watershed (5.6% of the watershed) have remained in row-crop production during the restoration period and are farmed on a cash-rent basis by local farmers. In these areas, improved agricultural manage-

Table 1. Summary of pesticide concentrations ($\mu\text{g/l}$) most commonly detected at the Walnut and Squaw Creek watershed outlets.

Compound	Parameter	Walnut Creek	Squaw Creek
Atrazine	Median	0.33	0.35
	Det. Freq. (%)	78%	80%
Cyanazine	Median	0.27	0.18
	Det. Freq. (%)	40%	36%
Acetochlor	Median	0.20	0.26
	Det. Freq. (%)	26%	34%
Deethylatrazine	Median	0.16	0.15
	Det. Freq. (%)	78%	80%

ment practices are mandatory, and all chemicals and application rates are approved prior to application to minimize adverse impacts on non-target plants and animals. In accordance with the Cropland Management Plan for the refuge: 1) no fall application of fertilizer is allowed; 2) a maximum of 45 kg of nitrogen per acre is allowed on conventional rotation corn acres; and 3) no pre-emergent herbicide is allowed (this includes common Iowa herbicides, atrazine, cyanazine, metolachlor, alachlor, metribuzin, and acetochlor).

Combining the prairie planting areas and restricted application areas, land use changes have been implemented on 22.4% of the Walnut Creek watershed. The remainder of USWFS land in the watershed consists of areas that have remained unchanged since refuge activities began in 1992. These lands consist of mainly grass or woods and comprise another 11.3% of the watershed. All told, the USFWS controls 1,759 ha, or 33.7%, of the Walnut Creek watershed above the WNT2 gaging station.

Beginning in 1993, with adoption of the Cropland Management Plan, pesticide and nitrogen use on refuge-owned lands was drastically curtailed. From 1992 to 1997, nitrogen applications in the Walnut Creek watershed were reduced approximately 18.1% over the six year period (Schilling and Thompson 1999). Pre-emergent pesticide use was eliminated on refuge-owned lands in 1993, reducing pesticide application in the watershed by an estimated 28%.

Water Quality

Pesticides. Six different compounds and two degradation products were detected between 1994 and 1999 in Walnut and Squaw Creek surface waters. Atrazine was by far the most frequently detected compound, as is true across Iowa, with the frequency of detection ranging between 78% to 80% in the main channels (Table 1). Concentrations ranged between <0.1 to $3.4 \mu\text{g/l}$ at Walnut Creek and <0.1 to $5.2 \mu\text{g/l}$ at Squaw Creek, with median concentrations at the downstream stations nearly equal ($0.33 \mu\text{g/l}$ vs. $0.35 \mu\text{g/l}$, respectively).

For statistical analyses of atrazine concentration and load data, concentrations reported as $<0.1 \mu\text{g/l}$ were considered to be one-half the detection limit ($0.5 \mu\text{g/l}$). Atrazine data were highly skewed and required log transformation before t-tests or regression analyses were conducted. T-tests found no significant difference between the means of atrazine concentrations and loads in the two watersheds ($P = 0.85$ and $P = 0.29$, respectively). (The term "load" refers to the amount of chemical mass in the stream and is the product of chemical concentration and discharge.) A comparison of atrazine loads at the Walnut Creek upstream and downstream gages suggested a possible reduction in atrazine loads between the upstream basin sampled at WNT1 and the remainder of the basin (subtracting the contribution of the upstream basin). Regression analysis of atrazine loads over time were not found to be statistically significant at the $P = 0.05$ level ($P = 0.15$). However, the calculated P-value of 0.15 between the

upstream Walnut Creek watershed at WNT1 and the remainder of the watershed (WNT2) suggested that a gradual decrease in atrazine loads may be occurring, but there was insufficient data to adequately substantiate or quantify the change. Subsequent data added to the existing data set may reveal the same trend at higher significance.

After atrazine, cyanazine was the most frequently detected pesticide with median concentrations $<0.3 \mu\text{g/l}$ (Table 1). Detection frequencies of cyanazine were nearly the same for both downstream main stem sites (36 to 40%). Both degradation products of atrazine were found with desethylatrazine (DEA) more commonly detected than deisopropylatrazine (DIA). Concentrations for both degradation products were generally below $0.2 \mu\text{g/l}$. Acetochlor was detected at approximately the same frequency in both basins with median concentrations from 0.20 to $0.26 \mu\text{g/l}$ (Table 1).

Nitrogen. Nitrate-N concentrations have ranged between 1.8 to 12.0 mg/l at the downstream Walnut Creek station (WNT2) and 2.1 to 15.0 mg/l at the downstream Squaw Creek stations (SQW2). Both basins showed a similar temporal pattern of detection and an overall reduction in nitrate-N concentrations from upstream to downstream monitoring station (Fig. 3). Higher concentrations were noted in the spring and early summer months coinciding with periods of application, greater precipitation and higher stream flows.

Decrease in nitrogen concentrations between upstream and downstream stations observed in both watersheds could be caused by biological uptake, denitrification, or dilution by water lower in nitrogen. Ratios of upstream to downstream samples for chloride and nitrate-N can be used to clarify which of these processes contributed to concentration differences. Ratios of one indicate no in-stream change in concentration between upstream and downstream stations, whereas ratios greater or less than one indicated additional inputs or reductions. In both Walnut and Squaw creeks, nitrate-N ratios were less than one, suggesting in-stream reductions caused by denitrification and biological processes (Fig. 4). However, in Walnut Creek, chloride ratios were also less than one, suggesting that inputs of both nitrate-N and chloride were reduced in this watershed. Reduced chloride inputs may be associated with decreased use of potassium chloride (KCl) fertilizer in the watershed or possibly dilution from other water sources (surface water or groundwater) with low chloride concentrations.

A t-test found a significant difference between the nitrate concentration means of the Walnut and Squaw creek data sets from 1995 to 1999 ($n = 82$, $P < 0.05$) with the overall mean nitrate concentration in Walnut Creek substantially lower than Squaw Creek (8.37 mg/l and 9.36 mg/l , respectively). Regression analysis was performed to determine if a change has occurred over time in the relationship of nitrate concentrations in the treatment watershed (Walnut) and the control watershed (Squaw). Regression residuals were calculated and plotted over time. If the relationship between treatment and control nitrate concentrations had not changed over time, then there

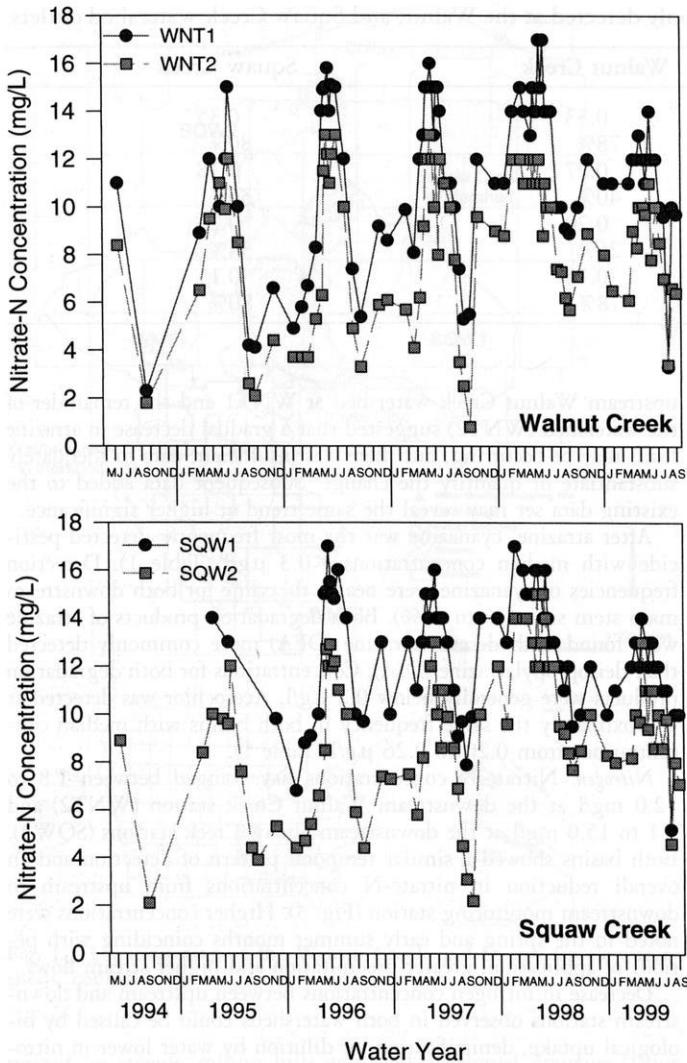


Fig. 3. Nitrate-N concentrations and upstream and downstream sampling sites in Walnut and Squaw creek for water years 1995 to 1999.

should be no apparent trend in the residuals over time and a best-fit regression line through the residuals should have a slope of zero. A plot of regression residuals showed the slope of the regression line to be statistically different from zero ($P = 0.03$) indicating a gradual decrease in nitrate concentrations at the Walnut Creek watershed outlet in relation to Squaw Creek watershed outlet (Fig. 5).

Analysis of nitrate concentration data between upstream (WNT1) and downstream (WNT2) locations on Walnut Creek was conducted using the same regression procedure. A slight decreasing trend in nitrate concentrations at WNT2 was evident ($P = 0.15$) but was not statistically significant at the $P = 0.05$ level.

Trends in nitrate concentrations over time between treatment and control watersheds and between upstream-downstream sites on Walnut Creek appear linked to increasing nitrate concentrations detected at both SQW2 and WNT1 sampling sites. Regression of nitrate concentrations over time indicated increasing trends at SQW2 ($P = 0.02$) and WNT1 ($P = 0.06$). Data from WNT2 were not significant ($P > 0.1$). Interestingly, the upstream sampling site on Squaw Creek also showed no evidence of increasing nitrate concentration over time ($P > 0.1$). Increasing divergence between treatment and control wa-

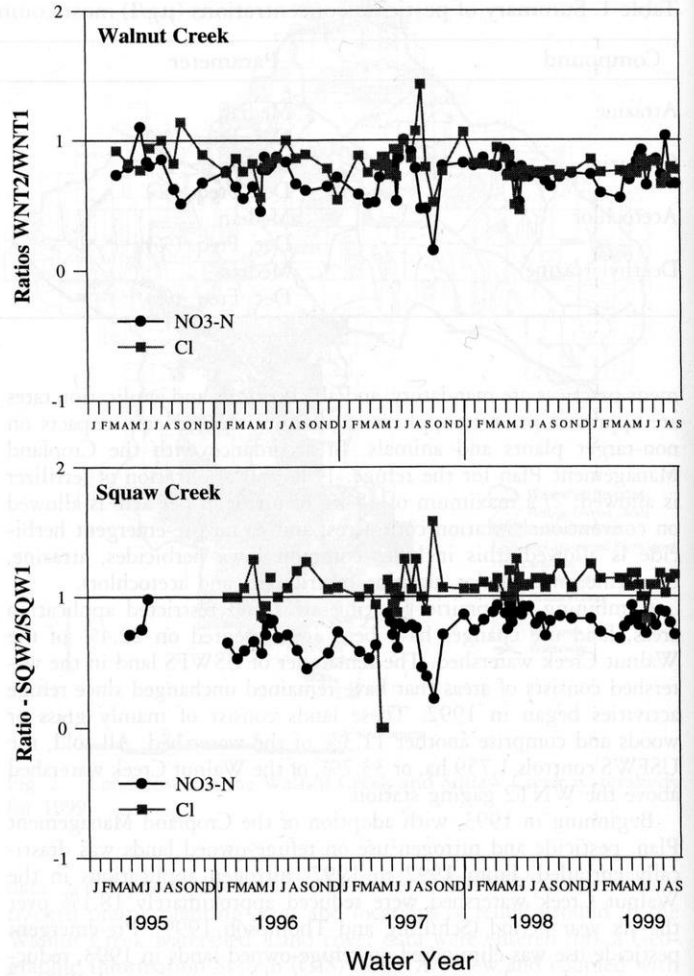


Fig. 4. Ratios between nitrate-N and chloride concentrations at upstream and downstream sampling sites in Walnut and Squaw creek for water years 1995 to 1999.

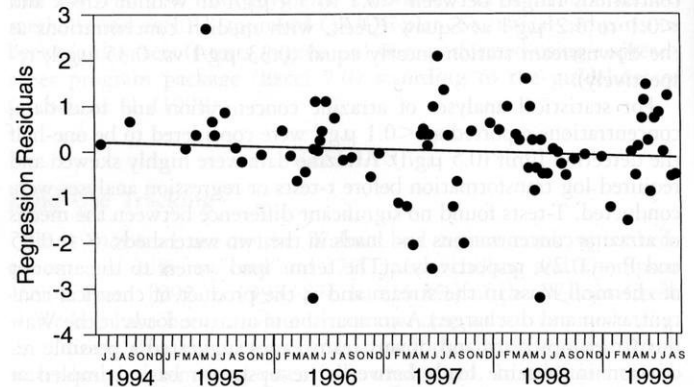


Fig. 5. Regression residuals plotted over time comparing nitrate concentrations in the treatment watershed (Walnut Creek) to the control watershed (Squaw Creek). The decreasing slope of the regression line was statistically different from zero ($P = 0.03$).

tersheds and upstream/downstream sites on Walnut Creek suggested that nitrate-N concentrations at WNT2 were not changing in the same manner as SQW2 or WNT1.

Although nitrate concentrations were decreasing in the Walnut Creek watershed relative to Squaw Creek, a decrease in nitrate loads between Walnut and Squaw creek watersheds was not apparent. Due to occasional high discharges, the nitrate load data were highly skewed and required log transformation for analysis. Regression of nitrate load residuals over time did not show change between the treatment and control watersheds ($P > 0.1$). Examining individual data points indicated that several spurious values could be traced to occasional large differences in rainfall amounts and runoff between the two watersheds. Large discharge events generated correspondingly high nitrate loads measured in one watershed and not the other, serving to reduce comparability. The median nitrate load ($n = 77$) in Walnut Creek and Squaw Creek was 19.0 kg/ha/yr and 21.7 kg/ha/yr, respectively. These loads were considerably higher than nitrate loads reported for pristine tallgrass prairie watersheds in Kansas (0.16 kg/ha/yr) (Dodds et al. 1996) but similar to loads reported for rangeland and cropland in Oklahoma (2–15 kg/ha/yr) (Oleness et al. 1975).

Considering that the Walnut Creek project is part of a long-term water quality monitoring program, an interesting question posed by the data is, How long did it take before changes in nitrate concentrations became statistically significant between treatment and control watersheds? Averaging about 20 water samples per year, more than three years of intensive data collection were needed (63 samples) before statistically significant changes were observed. After the first three years of sampling (June 1994 to September 1997), nitrate data showed no change over time between the two watersheds ($P = 0.69$). Only after the length of time and number of samples increased sufficiently was the statistical range large enough for changes to be detected.

DISCUSSION

The Walnut Creek Watershed Monitoring Project began with the expectation that conversion of row crop to native prairie and improved cropland management would result in measurable improvements in surface water quality. Water quality improvements were hypothesized because of the substantial decrease in nitrogen fertilizer and pesticide applications on refuge-owned lands. Completion of the first five years of full-scale monitoring (1995–1999) has shown a small, but statistically significant, reduction in nitrate concentrations at the Walnut Creek watershed outlet in relation to Squaw Creek. However, no differences in atrazine concentrations or nitrate and atrazine loads have been observed between treatment and control watersheds. With the magnitude of land use change implemented in the Walnut Creek watershed, should greater water quality improvements be expected?

Are Further Improvements Coming?

Indications of change provided by the nitrate data suggested that large-scale land conversions from row crop to prairie are improving water quality in the Walnut Creek watershed. The expectation for nitrate concentrations in the foreseeable future is continuation of this trend with increasing divergence from the control watershed. The fact that the increasing divergence may be due, in part, to increasing nitrate concentrations at SQW2 and WNT1 should not diminish the effect that land use changes are having on nitrate concentrations in the Walnut Creek watershed. In areas where land use practices have not changed since 1992 (Squaw Creek watershed and lands located above the WNT1 sampling site), nitrate concentrations in surface water have been slowly increasing over time. However, at the

Walnut Creek watershed outlet, concentrations have shown no change over time, suggesting that the prairie restoration activities concentrated in the lower portion of the Walnut Creek watershed appear to have halted an otherwise increasing trend.

Changes in nitrate concentrations over time between treatment and control will be considerably easier to track than pesticides due to differences in chemical delivery to streams. In Iowa, groundwater seepage and tile discharge is the primary source of nitrate to streams (Hallberg 1987). Monthly nitrate concentrations tend to be normally distributed in any given year. Nitrate concentrations in Walnut and Squaw creeks have followed this pattern, allowing for easier comparisons between paired data. However, the manner in which nitrate is delivered to streams can often result in a substantial lag time before changes in application rates can improve water quality. In many groundwater systems, considerable time is needed for nitrate, leached from cropped fields, to move as shallow groundwater to streams. In the Walnut and Squaw creek watersheds dominated by low permeability glacial materials, groundwater flow is exceedingly slow. Average groundwater flow velocity in the Walnut Creek drainage way was estimated to be 6.7×10^{-7} m/s (Schilling and Wolter 2001). Based on this velocity, groundwater flows approximately 21 meters per year. Thus, during the five-year period of nitrate monitoring (1995 to 1999), a zone of about 105 meters on either side of the main stem and tributaries would have contributed to baseflow discharge in the Walnut Creek watershed. Therefore, it should come as no surprise that changes in nitrate concentrations between Walnut and Squaw creek watersheds have taken considerable time to detect.

Pesticide concentrations, on the other hand, are primarily delivered to streams via runoff. Because of this, concentrations typically show a high degree of variability when they are detected (if at all), making trends in concentration difficult to detect over time. Depending on the timing of sample collection in relation to storm events and application periods, pesticide concentrations can vary orders of magnitude. Overall, the high degree of variability in atrazine concentrations as well as the number of observations below the measurable detection limit (20% of atrazine observations) will make detecting changes in atrazine difficult over the course of the project. Nonetheless, monitoring will continue for pesticides and perhaps show indications of improvements with additional data.

Does Watershed Size Matter?

Another factor to consider in evaluating water quality improvements on a watershed scale is the size of the watershed. Is it possible that the sizes of the Walnut and Squaw Creek watersheds have made detecting changes more difficult? The downstream monitoring site in Walnut Creek integrates water contributions from a large landscape area and does not isolate areas of change. When areas of land use change were isolated at a subwatershed scale, substantial water quality differences were observed between subwatersheds dominated by restored prairie versus row crop (Schilling and Wolter 2001). A synoptic surface water sampling event conducted in 1999 in the Walnut Creek watershed found concentrations of nitrate, chloride and atrazine substantially lower in subwatersheds draining primarily restored prairie (<1 mg/l, <3 mg/l, and <0.1 mg/l, respectively) compared to subwatersheds draining predominantly row crop areas (concentrations of nitrate, chloride and atrazine were typically >8 mg/l, >12 mg/l and >0.3 mg/l, respectively) (Schilling and Wolter 2001). However, when these water quality differences between end member concentrations (prairie versus row crop) are integrated over an entire watershed, the differences become difficult to detect.

Climatic factors also play a role obscuring water quality comparisons, particularly for pesticide concentrations and chemical loads (nitrate and pesticides). Although the paired watershed approach was

designed to minimize climatic factors, variations in rainfall intensity and runoff between the paired basins will continue to make comparisons problematic.

Where Are Land Use Changes Occurring?

A final issue to address in evaluating the effectiveness of prairie restoration in Walnut Creek to improve watershed water quality is the location of the refuge within the watershed. Should water quality improvements be expected when land use changes occur in the core of the watershed rather than headwater areas? Currently, nearly all of the patchwork assemblage of prairie restoration and land management controls are located in the core of the watershed near the Walnut Creek channel rather than in the headwater areas of the basins and subbasins. Headwater areas in both Walnut and Squaw creek basins are more highly row cropped than the remainder of the watersheds, averaging more than 80%. Headwater areas are also more heavily tiled compared to the rest of the watershed, and pesticides and nitrogen are still being applied at normal rates in these areas. Perhaps water quality differences between the treatment and control watersheds are difficult to detect due to the contribution of headwater areas to the main channel.

The Walnut Creek Monitoring Project began with an ambitious goal to implement a water quality program to document water quality improvements resulting from large-scale watershed restoration and management. After five years of monitoring, there are indications of water quality improvements that will be followed in the coming years. The Walnut Creek Monitoring Project clearly demonstrates the need to follow projects for several years in order to begin to see changes. Only by establishing a long-term monitoring record can the effects of restoration activities on water quality in the Walnut Creek watershed be fully evaluated and quantified.

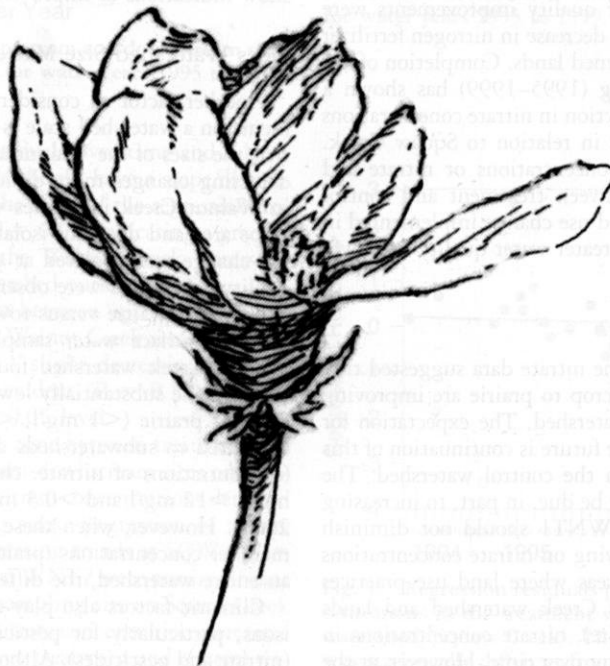
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The Cajun Prairie Restoration Project

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The Cajun Prairie is that part of the coastal tallgrass prairie found in southwestern Louisiana. With less than 40 ha remaining of the original 1,000,000 ha, it is possibly the most imperiled ecosystem in North America. A restoration project was initiated to see if prairie restoration techniques used elsewhere could be successfully employed in southwestern Louisiana. In 1988, restoration of 4 ha began in the city of Eunice. Seeds were hand-collected from local railroad prairie remnants. Seeds were broadcast following site preparation. Additional plants were propagated in containers from roots, stems, and seeds and then transplanted. Sods were removed from remnants to protect plants and to inoculate the site with the soil biota of native prairie. Prescribed winter burns of the site were conducted annually. In a 1995 census, more than 250 species of prairie plants were established. In a 2000 census, aggressive, early succession plants (native and exotic) had disappeared. In 2000, diameters of clumps of colonial prairie plant species were measured; average annual increase ranged from 8.3 cm to 91.3 cm. This experimental restoration project demonstrates that restoration of Cajun prairie is feasible. The project is an important repository for locally adapted prairie ecotypes and a model for other restoration efforts being attempted.

INDEX DESCRIPTORS: Cajun Prairie, tallgrass prairie, prairie restoration, Louisiana.

The western Gulf of Mexico coastal plain is known for its diverse habitats and wildflowers (Brown 1972, Ajilvsgi 1979, and Tveten and Tveten 1993). The region is characterized by marshes, prairies, savannas, bottomland hardwood, and upland pine forests. A major feature is the coastal tallgrass prairie (Allain et al. 1999, Smeins et al. 1992). The Cajun Prairie is part of the coastal tallgrass prairie found in southwestern Louisiana (Allen and Vidrine 1989, Allain and Johnson 1997, Allain et al. 1999, Allain and Castille 2000). Cajun Prairie annual rainfall frequently exceeds 1.25 m. Short winters and long summers expand current concepts of North American prairie. Several plant species occur in this prairie that do not occur in prairies elsewhere. Less than 40 ha of the 1,000,000 ha of pre-settlement prairie in southwestern Louisiana remain, making Cajun Prairie one of the most imperiled ecosystems in North America (Allain and Johnson 1997). The remaining prairie exists primarily as remnants along railroad rights-of-way, each sustaining its own assortment of native plants and animals and each surviving a variety of assaults. In a period of only five yrs, from 1995 to 2000, remnant area has been halved. Despite the scarcity of this ecosystem, our surveys of these remnants uncovered more than 600 species of plants and hundreds of insect species (Allen and Vidrine 1990, Vidrine and Allen 1993, Allain and Castille 2000). A restoration project was initiated to see if prairie restoration techniques used elsewhere could be successfully employed in southwestern Louisiana.

METHODS

In 1988, the city of Eunice, Louisiana leased a 4 hectare lot from Union Pacific Railroad for the purpose of reconstructing prairie in the city limits of Eunice (The Cajun Prairie Restoration Project).

Also, the Cajun Prairie Habitat Preservation Society was created to preserve and restore this ecosystem. A number of local agencies cooperated in this effort (Allen and Vidrine 1989, Vidrine et al. 1995). In September, 1988, the site was mowed and herbicided with glyphosphate. After plant senescence, a prescribed burn was conducted to remove biomass.

In the fall of 1988, seeds were collected from local prairie remnants along railroad rights-of-way. Most of the seeds were collected by students from local schools and clubs. The seeds were stored dry at 4°C until the day of planting but received no other treatment. Since most of the seeds were collected during the autumn, the majority of the seeds were from summer and autumn bloomers. Sod was rescued from remnants in danger of destruction by hand digging. Plants were propagated in containers from cuttings and seeds.

On 9 December 1988, the seeds were distributed by hand by the individual who had collected them producing a heterogeneous distribution. The area was then harrowed in order to work the seeds into the soil. The following two winters, hand-collected seed was sown into bare areas. At the same times, plants grown in containers and sods from remnants were transplanted into sites that were selected based upon soil moisture patterns. The sods added additional species as well as inoculated the soil at the site with the soil biota of the native prairie.

Burns were conducted annually beginning in 1989. Minimal weeding was done. Removal of Chinese tallow trees (*Sapium sabifera*) is proving to be the greatest obstacle, requiring a tremendous amount of time. Tallow trees initially invade wet areas where there is often little fuel. They also invade disturbed areas in prairie. At only three to five yrs of age they suppress fuel and are no longer controlled by fire (Grace 1998). If the trees are left to grow, they are

Table 1. Plant species suitable for use in planting matrix for prairie restoration in Louisiana. In some cases, several species in a genus are listed as a single entry and separated by a front-slash. An asterisk indicates aggressive colonizers.

Grasses:

Andropogon gerardii
Panicum virgatum
Paspalum plicatulum
*Schizachyrium scoparium**
Sorghastrum nutans
Tripsacum dactyloides
 Forbs:
Arnoglossum ovatum
*Aster concolor/hemisphericus/patens**
*Baptisia alba/bracteata/nuttalliana/sphaerocarpa**
*Bidens aristosa**
*Chamaecrista fasciculata**
Coreopsis lanceolata/pubescens/tripteris
*Eryngium yuccifolium**
*Euthamia leptoccephala/tenuifolium**
*Gaura lindheimeri**
*Helianthus angustifolius/mollis**
*Lespedeza capitata/virginica**
Liatris acedotalis/squarosa
*Liatris pycnostachya/spicata**
*Monarda fistulosa/lindheimeri/punctata**
Pityopsis graminifolia
*Pycnanthemum tenuifolium**
*Rudbeckia hirta**
Silphium gracile/lacinatum
Solidago nitida/odorata/rugosa
*Tephrosia onobrychoides**

very difficult to eradicate. Birds eat their seeds and disperse them in their droppings, providing ample opportunity for this invasive weed to get established (Grace 1998).

The project was evaluated by conducting a census in 1995 and again in 2000. Relative abundance of plant species was determined from observation and analysis of photographs. Also, in 2000, diameters of clumps of colonial prairie plant species were measured along their greatest axes. Average annual increase in clump diameter was determined for six species (four grasses and two forbs).

RESULTS

The 1995 census estimated that half of the site was dominated by native prairie plants (Vidrine et al. 1995). More than 250 plant

species of the nearly 600 known from nearby remnants were established. Remaining portions of the site, most at lower elevations, succumbed to exotic vegetation, primarily the Chinese tallow tree. Exotic species that became established at higher elevations were eventually excluded from the site. General evaluations in 1995 and 2000 demonstrated that succession was occurring. A number of aggressive, early succession natives were either no longer evident or greatly reduced. Some of these included: *Agalinis* spp., *Ambrosia* spp., *Aster praealtus*, *Bidens aristosa*, *Croton capitatus*, *Chamaecrista fasciculata*, *Erigeron philadelphicus*, *Eupatorium* spp., *Euthamia* spp., *Helianthus angustifolius*, *Ipomoea* spp., *Passiflora incarnata*, *Ranunculus* spp., *Senecio glabellus*, and *Solidago canadensis* (Vidrine et al. 1995 and 2000, Allen 2000). Exotics that were excluded from well-drained sites include *Verbena brasiliensis* and *Paspalum urvillei* (Vidrine et al. 1995 and 2000, Allen 2000).

Several new species have appeared and flowered in the last five yrs including *Asclepias longifolia*, *Asclepias obovata*, *Ctenium aromaticum*, and *Pteroglossaspis eristata*. Due to the isolation of the site, these conservative species are thought to have been present either in the original seed mix or in the sod. However, germination and/or flowering was delayed.

Borsari and Vidrine (1997) examined the clump-size increase in six major species of plants in the site. These clumps were again evaluated in 2000, and the resulting data are summarized in Table 2. Ten growing seasons have been completed since the original sods were placed at the site. No fertilizer, watering, or other intervention other than fire have affected the plants to our knowledge. The results clearly depict that the sod-forming plants that appear as clumps can be readily examined and measured. The larger clumps have disintegrated in their centers, and numerous other native plants are now growing in and among the separate sprouts. Of the measured species, the fastest growing grass was *Tripsacum dactyloides* (eastern gama grass) with an average annual increase of 15.6 cm. The fastest growing forb was *Pycnanthemum muticum* (mountain mint) with an average annual increase of 91.3 cm. The slowest growing grasses were *Andropogon gerardii* (big bluestem) and *Sorghastrum nutans* (Indiangrass) with average annual increases of 8.3 and 8.4 cm, respectively. All six species appeared to increase in diameter continuously; thus, measurements were confined to plants with this life history strategy. In contrast many other species, e.g., *Coreopsis lanceolata* (lanceleaf tickseed), *Schizachyrium scoparium* (little bluestem), and *Schizachyrium tenerum* (slender bluestem), formed distinctive clumps of a limited size. Recruitment by seed may be more important for these species. The two life history strategies are obviously important in the overall restoration process as evidenced by events in plant succession at the site.

DISCUSSION

Successful establishment of a diverse perennial prairie community on the well-drained portion of this site clearly demonstrated that

Table 2. Clump-size estimates for six major matrix plants at the Cajun Prairie Restoration Project in Eunice, Louisiana. The diameters for the initial sod plugs were estimated in 1989 as they were planted. In 2000, the mean and standard deviation of the clumps for each species, the range of diameters measured, and the average increase in diameter per year of growth for each species are provided. The number is the number of clumps measured; all other measurements are in centimeters.

Species	Number	1989	2000	2000	Average
<i>Andropogon gerardii</i>	34	20	103 ± 29	58–194	8.3
<i>Sorghastrum nutans</i>	9	20	104 ± 37	53–180	8.4
<i>Panicum virgatum</i>	26	20	145 ± 33	67–200	12.5
<i>Tripsacum dactyloides</i>	15	20	176 ± 32	120–240	15.6
<i>Pycnanthemum muticum</i>	7	20	933 ± 269	660–1400	91.3
<i>Helianthus mollis</i>	24	20	332 ± 88	190–520	31.1

restoration of Cajun Prairie is feasible. However, it appeared that determining site suitability and matching species to site conditions are critical parts of restoration planning (Allain and Castille 2000). Most exotic and early succession plant species have been displaced as succession occurs in the restoration (Allen 2000, Vidrine et al. 2000). After six yrs, insect diversity in the restoration site resembled that of remnant prairies (Allen and Vidrine 1990, Vidrine and Borsari 1999). This indicated that, to some extent, ecosystem complexity was recovering.

The process of planting prairies involves both the selection of plants and the proper placement of plants in the site. An initial planting of seeds of native species that rapidly colonize cultivated restoration sites is referred to as a restoration matrix (Betz 1986). These early succession species facilitate future colonization of the site by conservative prairie plant species typical of later successional seres (McClain 1997). Table 1 provides a list of Cajun Prairie matrix species for future prairie restorations in southwestern Louisiana. These native plant species were very successful during the first 10 yrs of restoration in Eunice. Some of these species have already disappeared from the restoration project in Eunice. An alternate model for restoration involves simultaneously sowing seeds of both early succession and conservative, late succession species (Schramm 1990). This latter method hypothesizes that the more conservative species will germinate by successfully competing with the early successional species after the site has matured. Further, this latter hypothesis contends that conservative species cannot be successfully introduced into a perennial matrix that excludes newcomers.

Either of the two methods or a combination of these strategies is recommended for future research avenues in the search for better methods of restoring prairies in Louisiana.

The Cajun Prairie Restoration Project provides a model for other restoration efforts in southwestern Louisiana. One of the greatest drawbacks for further projects is the availability of local seeds and propagules of native plants. Because there are no remnant prairies in Louisiana being preserved, the importance of restorations as reservoirs of locally adapted ecotypes is immeasurable. Remnants are rarely burned, facilitating the rapid spread of Chinese tallow, a great cause for alarm (Grace 1998).

The Cajun Prairie Restoration Project provides a habitat for the development of a diverse and dynamic biological community. The project has provided opportunities for varied kinds of research. Borsari and Shirley (1993) examined the soil profiles after only three yrs into the restoration process of development and clearly demonstrated an accumulation of organic matter in the restoration site. This evidence indicates the impact that the prairie plants have upon soils in maintaining and generating soil fertility nutrients. Vidrine and Borsari (1998 and 1999) developed philosophical models for agriculture and for integrated pest management using Cajun Prairie vis-à-vis the Cajun Prairie Restoration Project for small farms and landscapes. The development of diverse insect and arachnid communities is obvious in the restoration site (Allain and Johnson unpubl. data, Vidrine and Allen 1993).

The paradigm of restoring habitat was developed by Aldo Leopold (Leopold 1949, 1999), and we continue this paradigm. However, there is a great need for more and larger projects, from gardens to farms to landscape scale restorations (Vidrine and Borsari 1998 and 1999, Jackson 1999, Vidrine et al. 1999a, b, and c, Semar and Vidrine 2000). This experimental project demonstrates that restoration of Cajun prairie is feasible. The project is an important repository for locally adapted prairie ecotypes and a model for other restoration efforts being attempted. Additional studies are critical if restoration and maintenance of this valuable community are to be successful.

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Successional Vegetation Dynamics on Pocket Gopher Mounds in an Iowa Tallgrass Prairie

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The successional dynamics of vegetation growing directly on gopher mounds in a northwest Iowa tallgrass prairie were investigated over a 2-yr period. One hundred gopher mounds produced during five time intervals were surveyed periodically in 1995 and 1996. The vegetation on mounds was compared to the vegetation growing in nearby undisturbed control quadrats. We found that vegetation cover, species richness, and species diversity all increased on mounds over time, but that each was significantly lower on mounds after 2 yrs of succession than in control quadrats. From the results, we projected that vegetation cover on mounds should recover to undisturbed levels by the third growing season, but richness and diversity may take from 6 to 11 yrs to recover. Forb species, small-seeded species, and short-lived species each composed a greater proportion of the species richness on mounds than in control quadrats. Most of the individual plant species found with greater frequency and cover on mounds were introduced exotics, while all those growing with greater frequency and cover in undisturbed areas were native perennials. These results are important for understanding the role of small disturbances in regulating species diversity and composition in tallgrass prairie plant communities.

INDEX DESCRIPTORS: gopher mounds, prairie, succession, disturbance.

Tallgrass prairie once covered vast expanses of central North America, but today less than one-tenth of one percent remains in some states and provinces of the eastern Great Plains (Samson and Knopf 1994). The fragmentation of the prairie landscape has caused a decline in diversity of the entire tallgrass prairie plant community (Noss 1987, Wilcove 1987) and also of the plant communities within remnants (Leach and Givnish 1996). One study on small prairie remnants in southern Wisconsin attributed the decrease in plant species richness over time to the suppression of fire, an important large-scale disturbance (Leach and Givnish 1996). Fragmentation of the prairie landscape has greatly reduced the occurrence of large-scale disturbances. Bison and elk grazing are non-existent on small prairie remnants, and fires occur only on carefully managed prairie tracts. Small-scale disturbances, however, have not been as greatly impacted by fragmentation and are still abundant on small prairie remnants. Thus, today it is more important than ever to understand the impacts of small-scale disturbances, alone and in combination with large-scale disturbances, on the plant species diversity and community composition of tallgrass prairie remnants.

Gopher mounds, which at our study site are produced by the burrowing activity of the plains pocket gopher (*Geomys bursarius*), are common small-scale disturbances on prairie remnants. Mounds are produced as pocket gophers tunnel underground in search of roots from preferred plant species (Andersen 1988, Behrend and Tester 1988) and periodically expel soil onto the surface. Mounds are approximately 0.60-m \times 0.40-m in size and are constructed repeatedly within a single growing season in clusters ranging over spatial scales of 1 to 20 m (Klaas et al. 2000).

Gopher mounds impact the plant community of prairie remnants at a variety of ecological scales. At the level of the entire plant community, research on shortgrass prairies has shown that above-ground plant production is higher in areas of gopher mound-building activity than in areas without mounds (Grant et al. 1980, Spencer et al. 1985). In addition, other research has shown that plant

species richness and diversity are higher in tallgrass prairies with gopher mounds present (Tilman 1983, Inouye et al. 1987, Huntly and Inouye 1988, Huntly and Reichman 1994). One study reported that species richness increased directly on small artificial soil disturbances (Reader and Buck 1991), but another reported that species richness can be significantly lower on individual mounds than in the surrounding undisturbed vegetation (Umbanhowar 1992).

Gopher mounds and other small disturbances also can affect the frequency and abundance of certain functional groups of plant species. For example, forb species have been found in greater abundance in areas of gopher mound-building activity than in undisturbed areas in shortgrass prairie (Williams and Cameron 1986, Martinsen et al. 1990). In addition, it has been demonstrated that small-seeded species exhibit greater survivorship in gaps than under competitive conditions with other plants (McConaughay and Bazzaz 1987). Another plant functional group, non-clonal species, was found to decrease significantly on tallgrass prairie remnants undergoing fire suppression (Leach 1990). Because clonal species are strong competitors that can prevent the establishment of non-clonal species in the absence of disturbance (Cook 1985, Sebens and Thorne 1985), gopher mounds could provide resources similar to fire in creating refugia for non-clonal species. Annual plant species, another functional group, have also been found in greater abundance in tallgrass prairies with gopher activity than in sites without gophers (Inouye et al. 1987), while perennial grasses as a group decreased in shortgrass prairies under conditions of high mound-building activity (Martinsen et al. 1990). In addition, both annuals and biennials are associated with regular and intermediate soil disturbances (Hart 1977), and Umbanhowar (1992) reported that annuals occurred with significantly greater frequency directly on small-mammal mounds than in the surrounding vegetation.

In addition to impacting vegetation at the levels of the plant community and functional groups, gopher mounds and other small disturbances can affect the frequency and abundance of certain in-

Table 1. Dates of mound creation and vegetation surveys, including ages of mounds at the time of survey in parentheses.

Mound Label	Dates Created	Survey Dates and Age of Mound (in months) at Time of Survey			
		June 1995	August 1995	June 1996	August 1996
June 1994	22 May–10 June 1994	12–16 June (12)	21–27 July (13.5)	11–26 June (24.5)	19 July–2 August (25.5)
August 1994	21 July–5 August 1994	21–23 June (10.5)	8–9 August (12.0)	11–26 June (22.5)	19 July–2 August (24.0)
June 1995	25 May–8 June 1995	—	18–21 July (1.5)	11–26 June (12.5)	19 July–2 August (13.5)
August 1995	13 July–27 July 1995	—	9–10 August (0.5)	11–26 June (11.0)	19 July–2 August (1.5)
June 1996	31 May–20 June 1996	—	—	26 June–1 July (0.5)	4–5 August (1.5)

dividual plant species. Plant species found in higher abundance on prairie remnants due to the presence of gopher mounds are often annuals that rely upon openings in the vegetation matrix for seedling survival (Goldberg and Gross 1988) or weakly competitive perennials that require bare space for seed germination and seedling survival (Gross and Werner 1982, Goldberg 1987). Individual species that increase in number directly on mounds or in the presence of mounds have been identified in earlier studies. For example, Platt (1975) identified a guild of fugitive plant species utilizing badger disturbances on tallgrass prairie. The species were all wind-dispersed and poor competitors that thrived on badger mounds because direct competition among them was reduced spatially and temporally in the open space of small disturbances (Platt 1975). In addition, Brotherson (1982) identified a group of individual plant species that increased in abundance on mima mounds [larger mounds also created by pocket gopher activity (Ross et al. 1968)].

The objective of this study was to investigate the direct response of a tallgrass prairie plant community to gopher mounds by recording the vegetation dynamics occurring directly on mounds undergoing succession. Much research has been conducted on the response of the plant community across whole prairie remnants to the presence of mounds (e.g., Tilman 1983, Inouye et al. 1987, Huntly and Inouye 1988, Huntly and Reichman 1994), but little work has been done investigating vegetation dynamics directly on individual natural disturbances (exceptions include Umbanhowar 1992).

We studied the plant community at three levels of organization: the entire plant community, functional groups of plants, and individual plant species. Community-level variables included vegetation cover, plant species richness, and plant species diversity. We predicted that vegetation cover, species richness, and diversity would be low on new mounds, but we were also interested in determining the time-scale over which vegetation would recover on mounds. We also predicted that species richness and diversity on mounds would eventually surpass the levels found off mounds.

At the functional group level, we investigated the successional response of four plant groups: forb species, species with small seeds, non-rhizomatous species, and short-lived species. We predicted that each functional group would grow in greater abundance on mounds than off mounds for many of the reasons cited earlier.

At the individual plant species level, we identified species growing with greater frequency or cover on gopher mounds than off mounds. We predicted that these species would represent the different functional groups investigated, particularly short-lived species.

METHODS

Study Site

The study was conducted in northwest Iowa at Anderson Prairie State Preserve (Emmet County; 43°26' N, 88°53' W), an 80-ha remnant of tallgrass prairie managed by the Iowa Department of Natural Resources. Anderson Prairie was grazed by cattle until the mid-1970s, but it was never plowed. At the time of this study, the prairie was managed with controlled fires set every 3 to 5 yrs. Vegetation on the site is typical of tallgrass prairie remnants and consists of approximately 150 plant species. The native grasses *Andropogon gerardii* Vitman and *Sorghastrum nutans* (L.) Nash are abundant and dominant. In addition, the exotic plant species *Bromus inermis* L. and *Trifolium pratense* L. were planted on the site when it was grazed and are abundant today. The animal community of Anderson Prairie appears to be typical of those found on prairie remnants in the central U.S., and includes the plains pocket gopher (*Geomys bursarius*).

In April 1994, a permanent 0.64-ha plot was established at the study site (Klaas et al. 2000). The plot consisted of 64 10-m × 10-m cells arranged in a square with no buffers between cells. The plot was characterized by a moderate elevational gradient, with the southwest corner approximately 6 m higher in elevation than the northeast corner. The soils across most of the plot consisted of the Nicollet and Clarion soil series (Jones 1997) indicating a long history of mesic prairie vegetation, while the northeast corner contained the Webster soil series (Jones 1997), indicative of wet-meadow vegetation. The majority of the plot remained relatively dry during the growing seasons and consisted of upland vegetation, while the northeast corner tended to remain wet after extended rainfall and contained some characteristic wet-meadow species (e.g., *Spartina pectinata* Link and *Fragaria virginiana* Duchn.). Gopher mounds were produced in abundance across the driest portions of the plot, while few mounds were produced in the northeast corner.

Successional Dynamics on Mounds

The 100 gopher mounds used in the study were produced during the following five time periods: June 1994, August 1994, June 1995, August 1995, and June 1996 (Table 1). The locations of all fresh mounds were recorded at 1-week intervals throughout the 1994, 1995 (Klaas et al. 2000), and 1996 growing seasons. Twenty mounds were chosen at random from all mounds created during each of the five time periods with the stipulation that mounds within a time period be separated by a minimum of 4 m. No restriction regarding minimum distance between mounds created during different time periods was imposed. During the study, no mounds were

created in the northeast corner of the plot, so the 100 surveyed mounds were randomly located within the southwest two-thirds of the plot.

Surveys of the vegetation growing on the mounds were conducted four times during the 1995 and 1996 growing seasons (Table 1). Hereafter, these surveys will be labeled as follows: June 1995 survey, August 1995 survey, June 1996 survey, and August 1996 survey. Mounds ranged in age from 0.5 to 25.5 months at the time of the surveys (Table 1).

Vegetation growing in control quadrats located off mounds was also surveyed in 1995 and 1996 for comparison with mound vegetation. Control quadrats were spaced at regular intervals across the plot, with one quadrat located within each 10-m × 10-m cell. All 64 of the quadrats were surveyed in 1995 from 27 June through 14 July. Due to time limitations, only 32 of the quadrats were surveyed in 1996, from 2 July through 15 July. These quadrats were located in every other cell across the plot. In addition, only quadrats located in cells with surveyed mounds were used in comparisons with mound vegetation, resulting in 49 of the 1995 and 25 of the 1996 control quadrats being used in analyses.

During each vegetation survey, a 0.6-m × 0.6-m quadrat was placed over each mound or control quadrat. The quadrat was slightly larger than many of the mounds, but only vegetation growing on the mounds was recorded. A plant species list was compiled for each quadrat, and a modified point-cover method was used to measure the percent cover of each plant species growing on a mound or in a control quadrat, including bare ground and plant litter.

Plant Community Variables

The following three variables were used to characterize the plant community on mounds and in control quadrats: vegetation cover, species richness, and species diversity. Vegetation cover was the proportion of each mound or control quadrat covered by vegetation. Species richness was a count of the number of species found per quadrat. Species diversity for each quadrat was calculated using the Shannon-Wiener diversity index:

$$H' = -\sum_{i=1}^S [P_i(\log P_i)]$$

where H' is the diversity index value, S is the number of species in the quadrat, and P_i is the proportion of each mound or control quadrat covered by each species (Peet 1974).

To determine how vegetation cover, species richness, and species diversity on mounds compared to the levels found off mounds, we compared the three variables on mounds at 2 yrs with the levels of the three variables found in control quadrats. The 2-yr mounds used in the comparison were the 40 mounds created during the June and August 1994 time intervals and surveyed in August 1996. The mounds were compared to the 25 control quadrats surveyed in 1996. The differences between vegetation cover and species diversity on mounds and in control quadrats were tested with Wilcoxon rank-sum tests (Cody and Smith 1991), and species richness was tested with a two-tailed t-test.

If the levels of these three community-level variables on 2-yr mounds were significantly less than the levels found in control quadrats, we estimated the length of time required for each to reach the control quadrat levels. Mean vegetation cover, species richness, and species diversity were calculated for each group of 20 mounds at each vegetation survey. Each variable was then plotted against mound age, and a log-linear model fit to the data. Assuming that cover, richness, and diversity would each follow the trajectory predicted by the log-linear models, we calculated the number of months for each to reach control quadrat levels. The 1995 and 1996 control quadrat surveys

were treated separately in the analyses because both vegetation cover and species diversity in the 32 quadrats surveyed both years were significantly different between the years (in pairwise t-tests, vegetation cover $P = 0.004$ and species diversity $P = 0.02$).

Plant Functional Groups

We characterized the response of the following four functional groups of plant species to mounds undergoing succession: forb species, species with small seeds, species with a non-rhizomatous growth form, and short-lived species. The forb species were classified as all species in families other than Poaceae and Cyperaceae. Species were classified as small-seeded if they produced seeds in which the longest seed axis is less than 3 mm in length, not including awns or other appendages. Descriptions of seeds in Montgomery (1977), Great Plains Flora Association (1986), Gleason and Cronquist (1991), and Davis (1993) were used to determine seed lengths. Non-rhizomatous species included all species described in Great Plains Flora Association (1986) that produce weak or no rhizomes. Species listed as annuals, biennials, or short-lived perennials in Great Plains Flora Association (1986) were classified as short-lived species. A complete list of functional group designations for all species in the study can be found in Wolfe-Bellin (1997).

Functional groups were quantitatively described as the proportion of all species on a mound or in a quadrat composed of species from a particular functional group. These values were calculated using the following equation:

$$P = \frac{n}{N}$$

where P is the proportion of species in a particular functional group within a quadrat, n is the number of species in the functional group in the quadrat, and N is the total species count in the quadrat.

To characterize the change in the proportions of each functional group on mounds undergoing succession, we calculated the mean functional group proportions for each group of 20 mounds at each vegetation survey. The functional group proportions on mounds and in the control quadrats were then plotted against mound age, and a log-linear model fit to the data. In these comparisons, 1995 control quadrat means were used, because the proportions of each functional group in the 32 control quadrats surveyed in 1995 and 1996 were not significantly different between the years (in pairwise t-tests, all P -values > 0.05) and because the 1995 control quadrat data provided a larger sample size.

In addition, we tested whether the functional group proportions differed significantly between mounds at 2 yrs and in control quadrats. For these tests, the 2-yr mounds were the 40 mounds created during June and August 1994 and surveyed in August 1996, while the controls were the 25 control quadrats surveyed during July 1996. The differences between proportion of forb species, small-seeded species, and non-rhizomatous species on mounds and in control quadrats were tested with two-tailed t-tests. Short-lived species were tested with a Wilcoxon rank-sum test because the data were not distributed normally (Cody and Smith 1991).

Individual Plant Species

The cover and frequency of each plant species were compared on mounds at 1 yr, on mounds at 2 yrs, and in control quadrats. Mounds at 1 yr consisted of those created in June and August 1994 and surveyed in August 1995. These mounds were compared to control quadrats surveyed in July 1995. The same mounds at 2 yrs, surveyed in August 1996, were compared to control quadrats surveyed in July 1996. The mean cover values for each species on mounds and in

control quadrats were tested for significant differences using Wilcoxon rank-sum tests (Cody and Smith 1991), while the frequencies with which species were found on mounds versus in control quadrats were compared qualitatively.

RESULTS

Plant Community Variables

Vegetation cover, species richness, and species diversity were each low on fresh mounds, increased rapidly within the first year after mound creation, and reached a plateau below the levels observed in undisturbed sites after 2 yrs (Fig. 1). After 2 yrs of succession on mounds, each variable was significantly lower on mounds than in the control quadrats (Fig. 1). The mean proportion of each 2-yr mound covered by vegetation was 0.91 ± 0.01 (Mean \pm 1 SE), while the mean proportion of each control quadrat covered by vegetation was 0.95 ± 0.01 ($z = 2.40$, $P = 0.02$). Mean species richness was 12.3 ± 0.5 on 2-yr mounds and 15.5 ± 0.5 in control quadrats ($t = 4.44$, $P = 0.0001$). Mean species diversity on 2-yr mounds was 0.799 ± 0.024 , while average species diversity in the control quadrats was 0.905 ± 0.027 ($z = 2.91$, $P = 0.004$).

For each of the community-level variables, a log-linear mathematical model adequately described the change in the variable as mound age increased ($P < 0.05$, Fig. 1). Assuming that continued mound succession for each variable would follow the trajectory of the model, the time required for each variable to reach the level found in control quadrats could be estimated. Recovery time estimates varied depending upon the year of the control quadrat survey used in the calculations. We estimated that vegetation cover could take between 28 months (using the 1996 control quadrat value of 0.952 ± 0.005) and 31 months (using the 1995 control quadrat value of 0.972 ± 0.005) to reach that of the control quadrats. Species richness on mounds was estimated to take from 70 months (approximately 6 yrs, using the 1995 control quadrat value of 14.4 ± 0.5 species) to 127 months (approximately 11 yrs, using the 1996 control quadrat value of 15.5 ± 0.5 species), while species diversity was estimated to take between 72 months (approximately 6 yrs, using the 1996 diversity level in control quadrats of 0.905 ± 0.027) and 106 months (approximately 9 yrs, using the 1995 diversity value of 0.931 ± 0.015) to reach levels in the control quadrats.

Plant Functional Groups

The proportion of vegetation on mounds composed of three of the four functional groups— forb species, small-seeded species, and non-rhizomatous species—increased on mounds undergoing succession (Fig. 2). For each of these groups, a log-linear mathematical model significantly fit the relationship between proportion of species on mounds composed of each functional group versus mound age ($P < 0.05$, Fig. 2). The proportion of the species on mounds composed of forbs, small-seeded species, and non-rhizomatous species was low when mounds were fresh, increased rapidly within the first year of growth, and leveled off at approximately 0.70, 0.38, and 0.36, respectively (Fig. 2). The proportion of species on mounds composed of short-lived species did not increase significantly over time and remained at approximately 0.10 from the time mounds were 0.5 months to 25.5 months of age (Fig. 2).

Forbs, small-seeded species, and short-lived species each composed a greater proportion of the vegetation on mounds after 2 yrs of succession than in control quadrats (Fig. 2). Forb species composed 0.68 ± 0.01 of the species on 2-yr mounds and 0.65 ± 0.02 of the species in control quadrats. Small-seeded species composed 0.36 ± 0.02 of the species on 2-yr mounds and 0.34 ± 0.02 of the species in control quadrats. The differences between the on- and off-mound

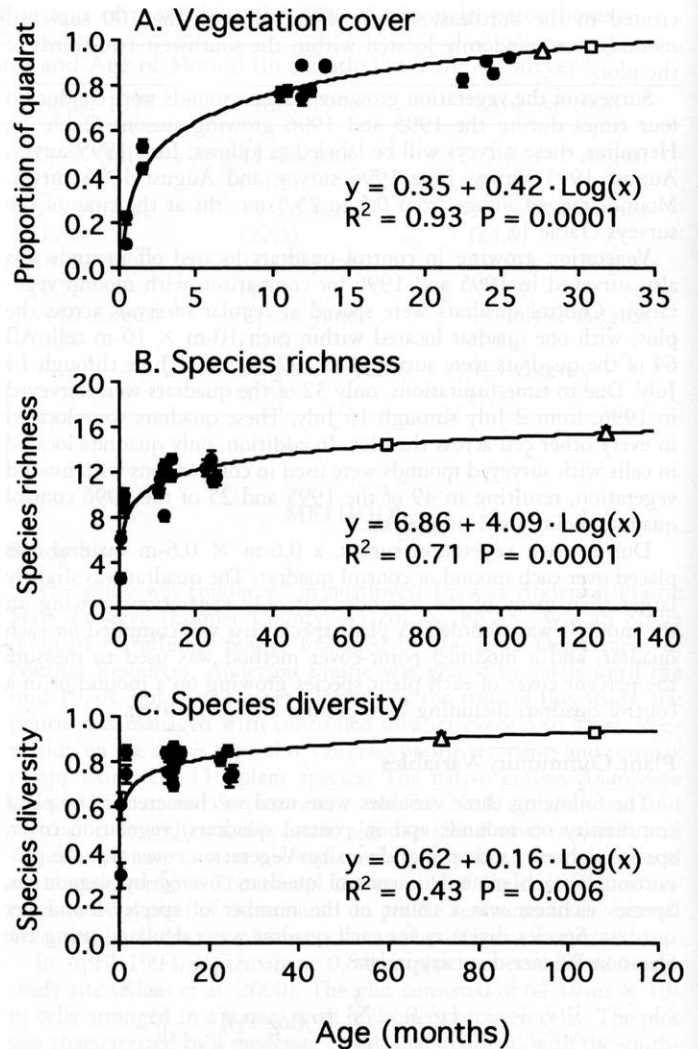


Fig. 1. Community-level variables on mounds and in control quadrats versus mound age. (A) Mean proportion of each mound or control quadrat covered by vegetation. (B) Mean plant species richness per mound or control quadrat. (C) Mean plant species diversity per mound or control quadrat. Solid circles represent mean values for each group of 20 mounds in a single survey class. Open squares and triangles are mean values for control quadrats surveyed in 1995 and 1996, respectively. Error bars are ± 1 SE. The best-fit log-linear model for each variable as a function of mound age is plotted. Only mound values were used in calculating the log-linear models. Control quadrat means are included on the graphs to provide visual estimates of the time required for each variable on mounds to reach the level in control quadrats. Note that the X-axis is a different length in each graph.

values, however, were not statistically significant for either forb species ($t = 1.31$, $P = 0.20$) or small-seeded species ($t = 0.85$, $P = 0.40$). The proportion of short-lived species was maintained at a constantly higher level on mounds than in control quadrats (Fig. 2D), and after 2 yrs of succession, short-lived species composed a significantly greater proportion of the species on mounds (0.06 ± 0.01) than in control quadrats (0.02 ± 0.01 , $z = -2.52$, $P = 0.01$).

Individual Plant Species

The 20 species with the highest average cover values both on mounds and in control quadrats are listed in Table 2. The six species

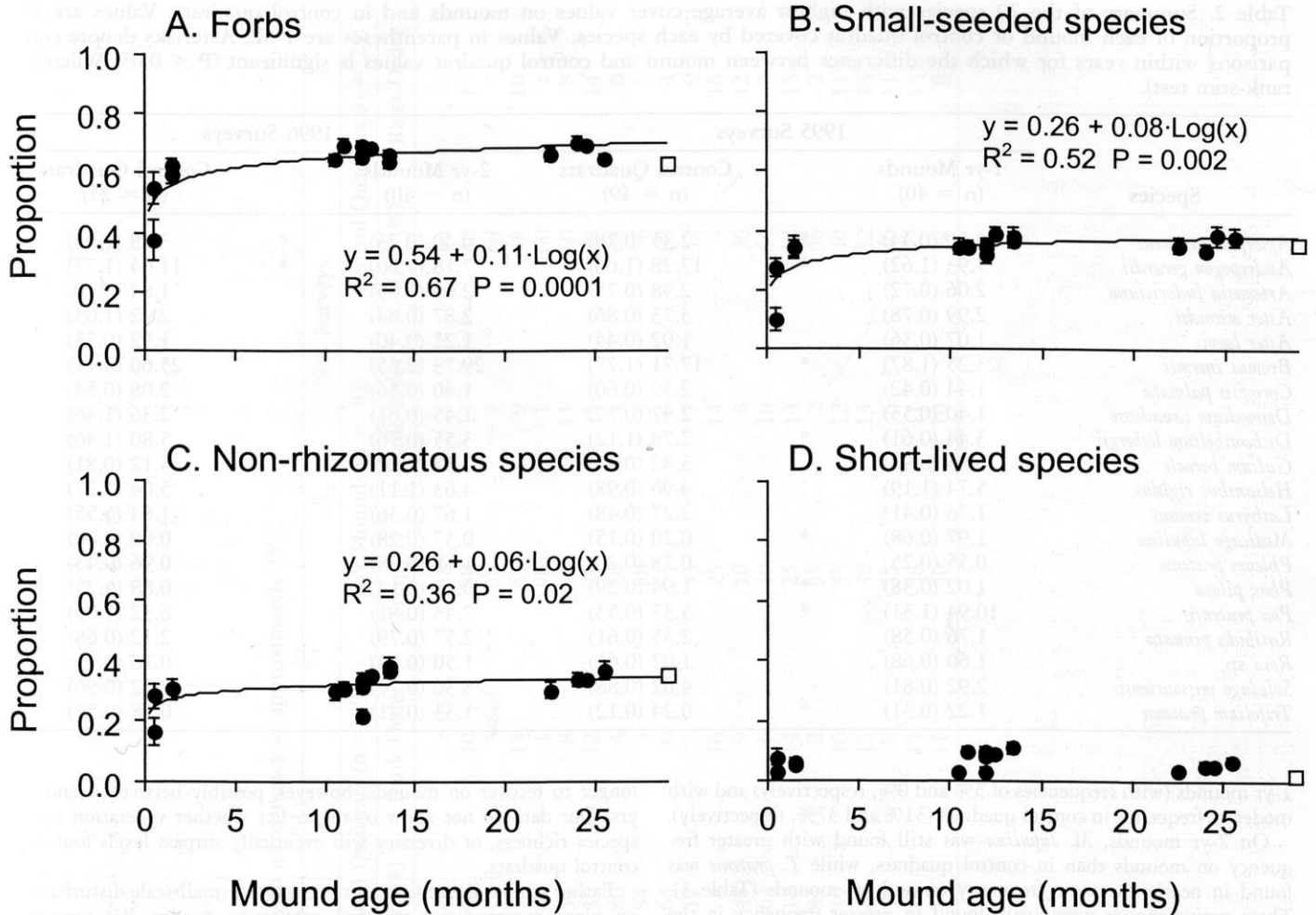


Fig. 2. Plant species functional groups on mounds and in control quadrats versus mound age. Mean proportion of all species per mound or control quadrat composed of (A) forbs, (B) small-seeded species, (C) non-rhizomatous species, or (D) short-lived species. All graphs and models were generated as in Fig. 1, except that only mean values for control quadrats surveyed in 1995 are plotted. In addition, control quadrat means are simply plotted at the far right on each graph and are not associated with a mound age. Only log-linear models which significantly fit the data are shown ($P < 0.05$).

with the greatest cover on 1-yr mounds—*B. inermis*, *Poa pratensis* L., *A. gerardii*, *Galium boreale* L., *Helianthus rigidus* (Cass.) Desf., and *Dichanthelium leibergii* (Vasey) Freckmann—also had high cover values in control quadrats (Table 2). The mean cover values of four exotic species—*B. inermis*, *P. pratensis*, *Medicago lupulina* L., and *T. pratense*—were all significantly greater on mounds at 1 yr than in control quadrats ($P < 0.05$, Table 2). On the same 1-yr mounds, the mean cover values of four native species—*A. gerardii*, *D. leibergii*, *Phlox pilosa* L. and *Amorpha canescens* Pursh—were each significantly greater in control quadrats than on mounds ($P < 0.05$, Table 2).

When the same mounds were surveyed in 1996 at 2 yrs of age and compared to control quadrats surveyed in 1996, the same species of high average cover in 1995 continued to dominate mounds and control quadrats (Table 2). The four exotic species continued to show greater cover values on 2-yr mounds than in control quadrats, but the differences were not statistically significant (Table 2). In the survey of 2-yr mounds, *G. boreale*, a native species, had significantly greater cover values on mounds than in control quadrats. The mean cover of *G. boreale* had been higher on mounds than in control quadrats when the mounds were 1 yr, but the difference was not statis-

tically significant. By the second year, the cover of *G. boreale* on mounds increased, while its cover in the control quadrats decreased slightly. The four native species with significantly greater cover values in control quadrats than on 1-yr mounds continued the same trend for 2-yr mounds, but the differences were significant for only two of the species—*A. gerardii* and *A. canescens* ($P < 0.05$, Table 2).

Plant species found on 1- and 2-yr mounds with a frequency of approximately 25% or greater are listed in Table 3. Species found in highest frequency on 1-yr mounds were nearly the same as those found in high frequency on 2-yr mounds and in control quadrats (Table 3). The six species with highest frequency on 1-yr mounds, 2-yr mounds, and in control quadrats included *A. gerardii*, *B. inermis*, *D. leibergii*, *G. boreale*, *H. rigidus*, and *P. pratensis*. On the 1-yr mounds, two exotic species, *T. pratense* and *M. lupulina*, had notably higher frequencies on mounds than in control quadrats (Table 3). On the same mounds, three native plant species—*A. gerardii*, *P. pilosa*, and *Aster ericoides* L.—all had moderate frequencies on mounds and high frequencies in control quadrats (Table 3). Two other native species, *A. canescens* and *Stipa spartea* Trin., were found only rarely on

Table 2. Summary of the 20 species with highest average cover values on mounds and in control quadrats. Values are the proportion of each mound or control quadrat covered by each species. Values in parentheses are 1 SE. Asterisks denote comparisons within years for which the difference between mound and control quadrat values is significant ($P < 0.05$, Wilcoxon rank-sum test).

Species	1995 Surveys		1996 Surveys			
	1-yr Mounds (n = 40)	Control Quadrats (n = 49)	2-yr Mounds (n = 40)	Control Quadrats (n = 25)		
<i>Amorpha canescens</i>	0.50 (0.44)	*	2.35 (0.78)	0.40 (0.23)	*	3.28 (1.08)
<i>Andropogon gerardii</i>	7.93 (1.62)	*	17.28 (1.66)	7.18 (1.60)	*	11.04 (1.77)
<i>Artemisia ludoviciana</i>	2.06 (0.72)		2.98 (0.75)	2.69 (1.05)		1.84 (0.70)
<i>Aster ericoides</i>	2.99 (0.78)		3.73 (0.86)	2.87 (0.84)		2.92 (1.03)
<i>Aster laevis</i>	1.07 (0.36)		1.02 (0.44)	1.21 (0.40)		1.92 (0.73)
<i>Bromus inermis</i>	23.25 (1.87)	*	17.71 (1.77)	29.73 (2.65)		25.60 (3.11)
<i>Coreopsis palmata</i>	1.44 (0.42)		2.59 (0.60)	1.40 (0.36)		2.08 (0.54)
<i>Desmodium canadense</i>	1.40 (0.53)		2.37 (0.79)	1.45 (0.61)		2.36 (1.46)
<i>Dichanthelium leibergii</i>	3.44 (0.61)	*	7.78 (1.12)	3.55 (0.76)		5.80 (1.46)
<i>Galium boreale</i>	5.85 (0.99)		3.82 (0.47)	7.32 (1.27)	*	3.12 (0.81)
<i>Helianthus rigidus</i>	5.74 (1.19)		4.96 (0.98)	4.63 (1.11)		5.04 (1.27)
<i>Lathyrus venosus</i>	1.76 (0.41)		2.27 (0.48)	1.67 (0.36)		1.64 (0.55)
<i>Medicago lupulina</i>	1.97 (0.68)	*	0.20 (0.15)	0.37 (0.28)		0.00 (0.00)
<i>Pbleum pratense</i>	0.55 (0.25)		0.78 (0.20)	1.15 (0.28)		0.96 (0.43)
<i>Phox pilosa</i>	1.02 (0.38)	*	1.94 (0.29)	0.48 (0.13)		0.88 (0.25)
<i>Poa pratensis</i>	10.94 (1.31)	*	5.37 (0.53)	7.43 (0.81)		6.32 (1.03)
<i>Ratibida pinnata</i>	1.76 (0.58)		2.35 (0.61)	2.57 (0.79)		2.12 (0.68)
<i>Rosa</i> sp.	1.60 (0.68)		1.02 (0.61)	1.50 (0.54)		0.76 (0.31)
<i>Solidago missouriensis</i>	2.92 (0.81)		4.02 (0.88)	3.36 (0.77)		2.52 (0.96)
<i>Trifolium pratense</i>	1.22 (0.31)	*	0.24 (0.12)	1.33 (0.41)		0.88 (0.56)

1-yr mounds (with frequencies of 5% and 0%, respectively) and with moderate frequency in control quadrats (31% and 37%, respectively).

On 2-yr mounds, *M. lupulina* was still found with greater frequency on mounds than in control quadrats, while *T. pratense* was found in nearly the same frequency on and off mounds (Table 3). Three native species were again found in greater frequency in the control quadrats than on mounds, but after 2 yrs of mound succession these species included *A. gerardii*, *P. pilosa*, and *H. rigidus* (Table 3). *A. canescens* and *S. spartea*, the two native species found in moderate frequency in control quadrats and low frequency on 1-yr mounds, continued to grow with greater frequency in control quadrats (40% and 28%, respectively) than on 2-yr mounds (10% and 3%, respectively).

DISCUSSION

The objective of this study was to investigate the direct response of a tallgrass prairie plant community to gopher mounds by recording the vegetation dynamics occurring directly on mounds undergoing succession. We found that the plant community on mounds differed from that in control quadrats at three levels of organization: the plant community, functional groups of plants, and individual plant species.

Three plant community variables—vegetation cover, species richness, and species diversity—were predicted to be low on fresh mounds and to increase as mounds aged, possibly reaching levels greater than those found in control quadrats. Instead, each increased as mounds aged, but still remained significantly lower on mounds than in control quadrats after 2 yrs of succession. Vegetation cover recovered the fastest and was predicted to reach the level found in control quadrats by the third growing season if succession continued to follow the log-linear trajectory predicted from the first 2 yrs of data. Species richness and diversity were predicted to take much

longer to recover on mounds, however, possibly between 6 and 11 yrs. Our data do not allow us to predict whether vegetation cover, species richness, or diversity will eventually surpass levels found in control quadrats.

Earlier studies documenting the effects of small-scale disturbances on plant communities reported conflicting results. For example, Grant et al. (1980) and Spencer et al. (1985) reported higher above-ground plant production in areas with gopher activity than in undisturbed areas. Other studies, however, found that vegetation cover was reduced in areas of mound-building activity (Foster and Stubbendieck 1980, Grant and McBrayer 1981), which matches the outcome in our 2-yr study. In addition, it has been reported both that plant species richness can be greater on soil disturbances (Reader and Buck 1991) and lower on small mammal mounds (Umbanhowar 1992) when compared to undisturbed sites, while other studies have reported that overall plant species diversity on prairie remnants increased with gopher activity (Tilman 1983, Inouye et al. 1987, Huntly and Inouye 1988, Huntly and Reichman 1994). These apparently contradictory results are similar to what we found in this study. Species richness and diversity remained low directly on mounds for at least 2 yrs, but the functional groups and individual species found in greater abundance on mounds and the environmental heterogeneity created by mounds could actually increase overall species diversity across the prairie (cf., Paine and Levin 1981).

Plant species from three of the four functional groups investigated in this study composed a greater proportion of the total species richness on mounds after 2 yrs of succession than in control quadrats. Forbs and small-seeded species initially constituted a small proportion of the vegetation on each new mound, but they increased over time and slightly exceeded the proportion found in control quadrats after 2 yrs. Neither group composed a significantly greater proportion of the vegetation on 2-yr mounds than in control quadrats, but

Table 3. Summary of all species found on 1-yr and 2-yr mounds with a frequency \geq approximately 25%.

Species	1995 Surveys				1996 Surveys			
	1-yr Mounds (n = 40)		Control Quadrats (n = 49)		1-yr Mounds (n = 40)		Control Quadrats (n = 25)	
	Freq (%)	Rank Order	Freq (%)	Rank Order	Freq (%)	Rank Order	Freq (%)	Rank Order
<i>Andropogon gerardii</i>	68	4	94	2	58	5	92	3
<i>Artemisia ludoviciana</i>	23	15	39	10	30	13	40	11
<i>Aster ericoides</i>	30	13	71	5	53	7	64	7
<i>Aster laevis</i>	30	13	14	15	45	9	48	10
<i>Bromus inermis</i>	98	1	100	1	98	1	100	1
<i>Coreopsis palmata</i>	30	13	51	8	38	11	60	8
<i>Desmodium canadense</i>	28	14	35	12	23	15	28	14
<i>Dichanthelium leibergii</i>	65	5	80	4	60	4	68	6
<i>Galium boreale</i>	85	3	84	3	88	3	76	5
<i>Helianthus rigidus</i>	60	6	63	6	55	6	80	4
<i>Lathyrus venosus</i>	50	8	57	7	53	7	52	9
<i>Medicago lupulina</i>	43	11	8	16	25	14	4	16
<i>Phelem pratense</i>	23	15	43	9	50	8	36	12
<i>Pbiox pilosa</i>	35	12	63	6	40	10	64	7
<i>Physalis virginiana</i>	30	13	18	14	25	14	12	15
<i>Poa pratensis</i>	88	2	94	2	95	2	96	2
<i>Ratibida pinnata</i>	28	14	39	10	33	12	40	11
<i>Rosa</i> sp.	28	14	24	13	30	13	32	13
<i>Solidago missouriensis</i>	45	10	57	7	55	6	40	11
<i>Trifolium pratense</i>	53	7	14	15	38	11	32	13
<i>Zizia aurea</i>	48	9	37	11	40	10	52	9

the growth trajectory of each indicated continued increases in their proportions on mounds. Short-lived species composed a fairly constant proportion of the species on mounds over time at a level greater than that found in control quadrats.

None of the functional groups were found at greater levels in control quadrats than on mounds, but this was expected since we chose *a priori* only functional groups that had been documented in earlier studies growing more abundantly in disturbed areas than in undisturbed areas. With this in mind, it is curious that non-rhizomatous species were found in similar levels both on and off mounds. Possibly a stronger effect on non-rhizomatous species would be seen with larger, more permanent disturbances. In addition, the response of small-seeded species to mounds was weaker than expected and could have occurred because we used a different criterion for determining seed size than previous studies. Most earlier studies using seed mass found that small seeds disperse further than large seeds and germinate under full light conditions (Baker 1972, McConnaughay and Bazzaz 1987, Peart 1989, Leach 1990). We used seed length to determine seed size, however, and short seeds may not necessarily disperse long distances or require full light for germination. In this case, the species included in the small-seeded functional group would not preferentially utilize mounds over undisturbed sites.

The individual species found with greatest frequency and cover on mounds were also those species found with greatest frequency and cover in the control quadrats. In this regard, it appears that mounds are largely recolonized by the dominant species in the surrounding vegetation matrix. We did, however, identify a suite of plant species growing with greater frequency and cover on mounds as compared to control quadrats and another set growing with greater frequency and cover in control quadrats when compared to mounds. All but one of the species found in greater abundance on mounds were exotics in the tallgrass prairie region; those growing with greater frequency and cover in control quadrats were all native perennials. The differences between mound and control quadrat cover and frequency values for most species were most pronounced on mounds after 1 yr of succession. By the second year, cover and frequency values on mounds either increased or decreased to resemble more closely the values found in control quadrats. One notable exception, however, was *A. canescens*, for which mound and control quadrat values for frequency and cover diverged as mounds aged.

In studies of longer-lived small disturbances, such as badger mounds, the plant species that responded with increased growth on disturbances were primarily native perennials (Platt 1975, Brotherson 1982). In this study and other studies of short-lived small disturbances, however, the plant species that responded to disturbance with increased growth tended to be exotic species or short-lived annuals and biennials (Reichman 1988, 1996; Wolfe-Bellin and Moloney 2000). Successful invasive species are likely to be good dispersers that can quickly colonize available sites (Bazzaz 1986), which could explain the greater frequency and cover with which exotic species grew on short-lived disturbances in this study. Native perennials that spread through extensive rhizome systems may grow continuously under conditions lacking disturbance, but they are removed, at least for a short time, from areas directly under gopher mounds.

The differences in vegetation between mounds and undisturbed areas could have an important impact on the spatial distribution of the plant community across prairie remnants. Gopher mounds are constructed repeatedly in clusters ranging over spatial scales of 1 to 20 m (Klaas et al. 2000). In addition, these clusters can be evenly spaced, causing hyperdispersion of mounds at spatial scales broader than 20 m (Klaas et al. 2000). The production of mounds in approximately the same locations over time creates areas of the prairie

with extremely different long-term disturbance regimes. Potentially, this could cause the distinctive plant community found on mounds to be maintained in some areas of the prairie undergoing high levels of small-scale disturbance, while vegetation characteristic of undisturbed areas could dominate in other areas.

In addition, the plant community on prairie remnants could be impacted by temporal variability in the succession on mounds. Some differences between the vegetation on mounds and in undisturbed areas are short-lived and will be maintained over time in the overall plant community only in locations where mounds are continuously produced. For example, most of the differences between individual species cover values on and off mounds appeared to be most pronounced after 1 yr of succession and were less distinct after 2 yrs. Other changes in the plant community can occur more permanently on single disturbances, however, and could be maintained even where mounds are produced only occasionally. The proportion of forb species and short-lived species, for example, appeared to remain higher on mounds than off mounds for at least 2 yrs.

As demonstrated in this paper, small-scale disturbances could potentially have a large impact on the plant community across prairie remnants through the successional vegetation dynamics occurring on individual mounds. Directly on mounds, vegetation cover, species richness and diversity, and the abundance of some native prairie species all decreased. On the same mounds, however, the abundance of a few exotic forb species and the proportion of forbs and short-lived species increased. In addition, the impacts of small-scale disturbances are not restricted to small spatial and temporal scales because pocket gophers repeatedly produce mounds in the same locations year after year with much variability in the levels of mound-building activity within and between years (Klaas et al. 2000). This results in highly disturbed areas of prairie within a matrix of relatively undisturbed vegetation, which can increase heterogeneity in the plant community across remnants (Tilman 1983, Inouye et al. 1987, Huntly and Reichman 1994) and maintain or increase plant species diversity. While large-scale disturbances, such as fire and grazing, have frequently been cited as important for the maintenance of species diversity on tallgrass prairie remnants (e.g., Leach and Givnish 1996), the importance of small-scale disturbances in regulating plant species diversity and community structure should not be overlooked.

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Comparison of Phenology, Photosynthetic Rates, and Leaf Morphology of Savanna and Prairie Populations of Shooting Star (*Dodecatheon meadia* L.)

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We compared leaf phenological development, photosynthetic rates under different levels of irradiance, and leaf morphology of populations of shooting star (*Dodecatheon meadia* L.) in burned savanna and burned and unburned prairie habitats. Rates of phenological development were significantly different between savanna and prairie populations, with the savanna plants completing their leaf development and senescence in less time than the prairie plants. Plants on the burned prairie had higher photosynthetic rates than plants on the burned savanna in early May 1994, although the photosynthetic rates of savanna plants were higher than the prairie plants by the late May sampling. In the 1994 and 1995 field seasons, the savanna plants maintained relatively consistent photosynthetic rates throughout the sampling period while plants from the burned and unburned prairie had decreased photosynthetic rates. In prairie habitat, shooting star plants responded positively to fire. Plants on the burned prairie had significantly higher photosynthetic rates than those on the unburned prairie, but differences in photosynthetic rates between plants from burned and unburned prairie decreased from early to late May. Prairie plants had leaves more typical of sun plants than savanna plants. Prairie plants had significantly larger leaf length to width ratios, greater specific leaf mass, and higher stomatal densities than savanna plants. The results of this study suggest that the differences in phenology, photosynthesis, and leaf morphology of shooting star plants growing in prairie and savanna habitats were likely related to varied environmental conditions between savanna and prairie habitats.

INDEX DESCRIPTORS: *Dodecatheon meadia*, shooting star, prairie, savanna, fire, photosynthesis, phenology, leaf morphology.

In the midwestern United States, savannas are transitional vegetation communities between the eastern deciduous forest and the tallgrass prairie in a climatic zone that can support grassland, savanna, and forest (Curtis 1971, Packard and Mutel 1997, Anderson and Bowles 1999). Fire frequency, which was related to topography, largely determined the historic occurrence of the three vegetation types (Anderson 1982, 1990). Prairies occurred on level to gently rolling landscapes that encouraged the spread of fire and burned nearly annually. Forests were associated with sheltered areas with dissected topography, which reduced fire frequency, and sites adjacent to waterways that served as fire breaks. Savannas occurred on sites that experienced fires at a frequency intermediate to that of the prairies and forests and contained fire-tolerant species from both communities (Curtis 1971, Risser et al. 1981, Nuzzo 1985, Packard and Mutel 1997, Robertson et al. 1997, Taft 1997, Anderson and Bowles 1999). Forest tree canopies mitigate extremes in environmental conditions in the ground layer (Geiger 1965, Turner and Quarterman 1968, Risser et al. 1981). However, the savanna tree canopy is patchy, creating open areas that favor ground layer species adapted to open habitats and shady areas under tree crowns favorable to species associated with forests. As a result, savannas contain species associated with prairie and forest habitats (Bray 1958, Bray 1960, Curtis 1971, Leach 1996, Taft 1997).

Forbs, non-graminoid herbaceous species, such as shooting star that mature in the spring, are strongly influenced by the dominant vegetation in prairie or savanna (Glenn-Lewin et al. 1990). In sa-

vanna, the heterogeneous tree canopy can create conditions that vary on temporal and spatial scales in the ground layer from those associated with open prairies to those similar to closed forests. For example, in the spring, before the savanna trees develop leaves, large areas under the tree canopies are exposed to full solar irradiance for much of the day. However, even when the foliage is fully developed, the heterogeneous tree canopy creates a patchy light regime in the understory, with full solar irradiance reaching the ground cover for varied periods of time depending upon local tree canopy density (Pruka 1994, Leach 1996). In unburned prairies, forbs initially develop in litter and standing dead vegetation that reduces irradiance and wind, maintains higher humidity than in open areas, slows the rate of soil warming, and reduces temperature fluctuation. On burned prairies, as shoots of the spring forbs emerge, they are exposed to full solar irradiance, higher wind speeds, faster rates of soil warming, greater temperature fluctuations, and lower relative humidity than forbs on the unburned prairies. As the grasses grow, they over top the spring forbs and mitigate environmental extremes so microclimatic differences between burned and unburned prairies tend to diminish (Old 1969, Peet et al. 1975, Knapp and Seastedt 1986).

This study was to provide insight into how a single species can occur in two somewhat contrasting habitats by studying shooting star in a burned savanna, and burned and unburned prairies. No unburned savanna was available, so a full factorial design of fire (burned and unburned) and habitat (prairie and savanna) was not possible. We examined: 1) the rate of phenological development, 2) photosynthetic rates, and 3) leaf morphology of shooting star plants in prairie and savanna habitats.

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METHODS

Study Areas

The phenological, morphological and physiological measurements were made on plants at the Weston Cemetery Prairie and ParkLands Foundation Merwin Nature Preserve. Weston Cemetery Prairie is a 2.1 ha mesic tallgrass prairie remnant located 15 km northeast of Lexington, Illinois (Johnson and Anderson 1986, Gustafson 1996). This site is surrounded on three sides by agricultural crops; to the north there is a railroad right-of-way with some remnant prairie also, which in turn is bordered on its north by another agricultural field. The management program includes a biennial burning regime, with one-half of the prairie burned each year. This burning regime allowed for the investigation of fire effects on shooting star. Weston burned and unburned prairie will be referred to as WBP and WUP, respectively.

ParkLands Foundation Merwin Nature Preserve is a 284 ha nature preserve located 7.0 km west of Lexington, Illinois (Gustafson and Anderson 1994) and 25 km southwest of the Weston Cemetery Prairie. The ParkLands savanna (PS) study site, which is approximately the same size as the Weston Prairie, is a remnant tallgrass savanna that is currently being restored to the pre-European settlement savanna condition. To open the canopy and encourage the growth of the remnant savanna ground layer species, the management program has included removal of selected trees and annual prescribed burns since 1988. Tree canopy cover is about 70% (Anderson et al. 1994). In addition to the savanna site, we made measurements (1994 only) on shooting star plants that were growing in the ParkLands Foundation restored prairie (PP). These plants were transplanted from the remnant savanna site in 1986. The restored prairie was managed with annual burning regime.

Study Species

Dodecatheon meadia (shooting star) is a C₃ perennial forb with an ephemeral-like seasonal growth cycle. In Illinois, vegetative buds that formed on the root crown during the previous season break dormancy over winter. A small rosette of leaves emerges above the soil in mid-March. Leaf development continues until mid-April, when flower buds form in the basal rosette. This development is shortly followed by elongation of the scape. Earliest flowers reach anthesis in early-May, and peak anthesis occurs in mid- to late-May. Young fruits develop in June as the leaves begin to senesce. Complete leaf senescence and fruit maturation occur in July, and mature capsules disperse seed by mid-August (Sorensen 1990).

Phenology

At the beginning of the 1993 growing season, a minimum of ten randomly selected shooting star plants were located and marked at the PS (10 April), WBP (10 April), and WUP (18 April). To monitor plant growth, maximum length and width of each leaf in the basal rosette were measured at weekly intervals. On all sampling dates at each of the three sites, 3–8 leaves that represented the range in leaf size were traced. A computer-aided imaging system was used to determine the area of each leaf tracing. Linear regression analysis was used to establish the relationship between the leaf surface area and the product of leaf length and width for each site: 1) PS-Y (leaf area cm²) = 1.83 + 0.065X (leaf length * leaf width); F_{1,26} = 4478, r² = 0.99; 2) WBP-Y = 13.10 + 0.063X, F_{1,24} = 2290, r² = 0.98; and 3) WUP-Y = 3.68 + 0.066X, F_{1,26} = 881, r² = 0.97, P < 0.001 in all cases. Senescence data were collected on the same plants by estimating the percent green leaf remaining at weekly intervals until complete senescence. To compare leaf development and senescence among PS, WBP and WUP, a rate of leaf develop-

ment and senescence (RLDS) index was calculated. The index was designed so that a single number could be used to indicate the extent to which the plants had completed their aboveground annual cycle of basal rosette growth and senescence. For each plant on each sampling date, the RLDS was the sum of the percent full leaf expansion (i.e. leaf development) in the rosette plus the percent non-green leaf (i.e. senescence), which was then divided by two. The RLDS ranged from 0% to 100%, with 50% indicating full leaf expansion and 100% indicating complete senescence and completion of the aboveground annual cycle.

Photosynthesis

After full leaf expansion, photosynthetic rates, stomatal conductance, transpiration rates, and environmental conditions (photosynthetically active photon flux density (PPFD), relative humidity, leaf and chamber temperature) were measured using the LI-COR 6000 gas exchange system at PS and PP (1994) and PS, WBP and WUP (1995). On each sampling date, measurements were made on shooting star plants during the hours of maximum solar irradiance (1100 to 1300 hours). Because the LI-COR-6000 did not have an internal light source, plants were exposed to direct sunlight at midday to measure the photosynthetic response to full irradiance. Within the savanna, plants were selected randomly from areas that received full irradiance during the sampling period. To achieve varied levels of irradiance at all sites, plants were covered with shade cloth to achieve approximately 50%, 25% and 10% of full irradiance. Measurements were made at each irradiance level (100, 50, 25, and 10%) on a single leaf from each plant, which remained attached to the basal rosette. Leaves were allowed to acclimate (5 min) at each irradiance level prior to photosynthesis measurements. Ten measurements were made over a two minute period for each leaf at each irradiance level. The mean of the 10 measures per variable (photosynthesis, PPFD, relative humidity, leaf and chamber temperature) was used in the statistical analyses. The LI-COR 6000 measures photosynthesis while the leaf chamber is the closed system mode. Consequently, photosynthesis measurements were recalculated using the LI-COR C6000 software package to correct for error associated with photosynthesis measurements being made in a closed system.

To test for differences between shooting star plants in savanna and prairie habitats while holding the fire treatment and habitat origin of the plants constant, we compared PS and PP plants using the 1994 data (n = 3). To test for fire effects, holding the habitat constant and minimizing genetic differences, photosynthetic rates of plants on WBP and WUP were compared. The PS plants were also included in the 1995 measurements (n = 4).

Leaf Morphology

Leaf morphology was determined by examining a leaf from 15 randomly selected plants at each of the three sites on 1 June 1995. To eliminate the effect of self-shading, only the top leaf of the rosette was collected from each plant. Leaves were preserved in formalin-acetic-acid (FAA), and stomatal densities and leaf thickness measurements were made using a light microscope equipped with a calibrated ocular scale. Stomatal densities (number/cm²) were determined on upper and lower surfaces of each leaf section using the mean value from three ocular field measurements made in the middle third longitudinal section of each leaf. Microscopic examination of 10 leaf cross-sections (infiltrated with deionized water, covered with immersion oil, and then a cover slip) was used to determine leaf thickness. Leaf surface area, length, and width were determined using a computer image process system (Nikon). Leaf mass per area (dry weight per unit area) was calculated based on the leaf surface area and the weight of the leaf, dried at 80°C for 48 hrs.

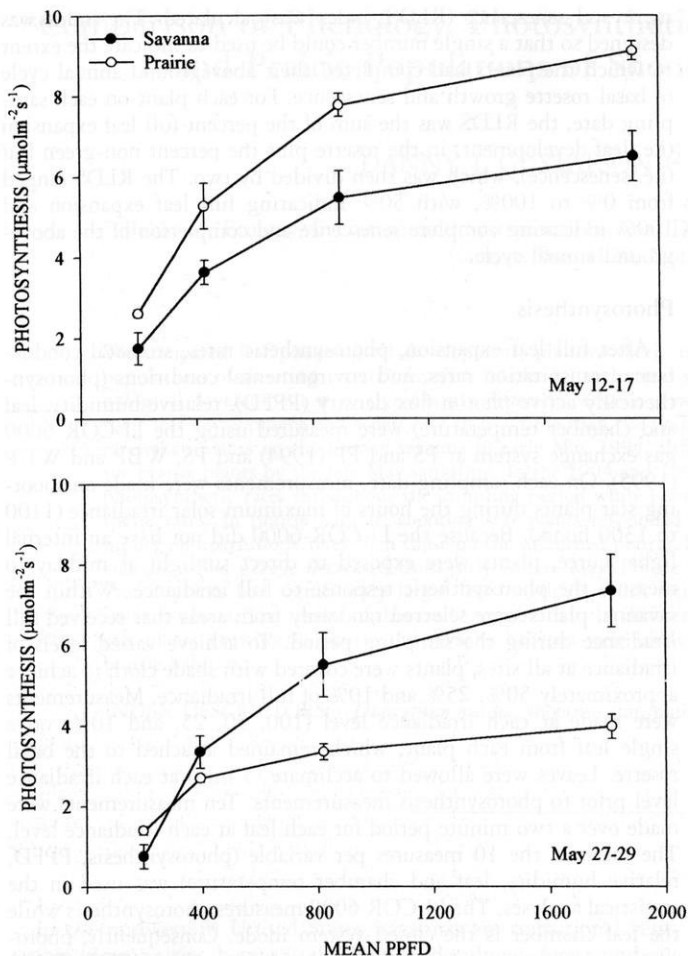


Fig. 1. Photosynthetic rates for ParkLands Savanna (PS) and ParkLands Prairie (PP) plants at four levels of irradiance in 1994. Values are means \pm one standard error.

Statistical Analyses

RLDS data from plants in PS, WBP, and WUP were compared over time using linear regression (SPSS PC 1990). Student's t-tests were performed to determine if there were significant differences among the regression slopes (Steel and Torrie 1960). Experimental error associated with the multiple student's t-tests was corrected using the Bonferroni method ($\alpha_e = 0.05/3 = 0.017$). For each sampling date, environmental conditions (relative humidity, leaf and chamber temperature, PPFD) were analyzed using two-way repeated measures analysis of variance (ANOVA) by site and date. For sampling dates when environmental conditions were not significantly different among the three sites, photosynthetic rates, stomatal conductance, and transpiration rates were analyzed using two-way repeated measures ANOVA by site and by shade level (SPSS PC 1990). One-way ANOVA and Tukey-honest significant difference post hoc tests (SPSS PC 1990) were used to test for differences among sites for leaf thickness, specific leaf mass, leaf length to width ratio, stomatal density, and leaf surface area. Data were transformed (log10, reciprocal, square root) to satisfy the assumptions of normality and equal variance. Statistical significance was accepted at $P \leq 0.05$.

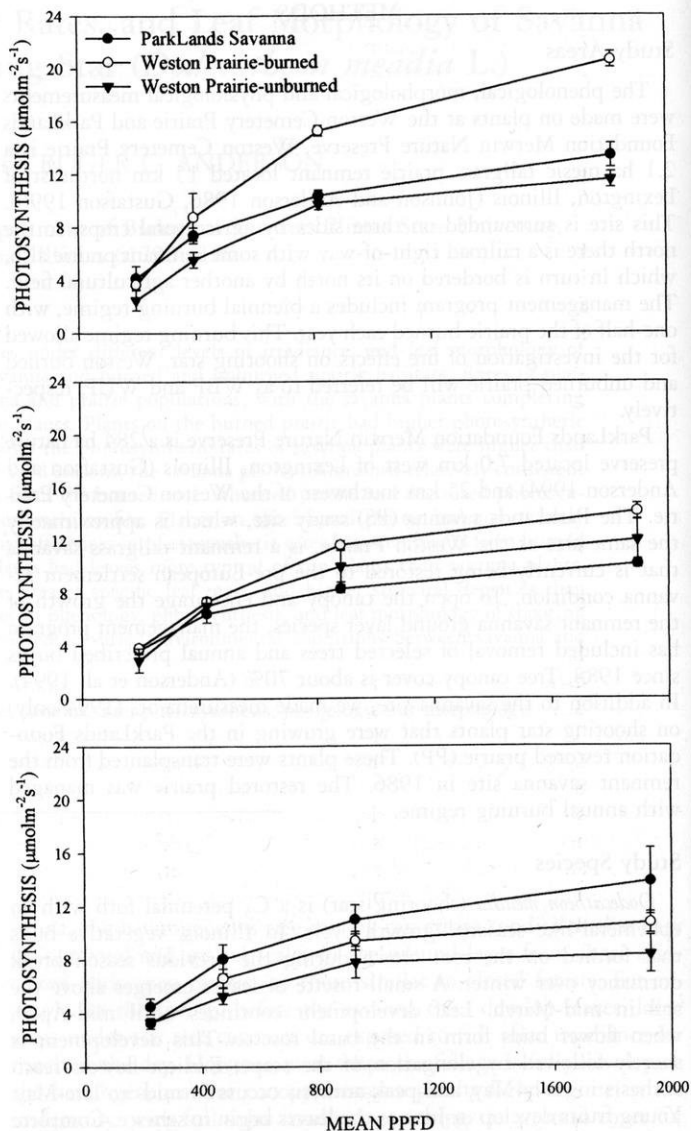


Fig. 2. Photosynthetic rates of plants from ParkLands Savanna (PS), Weston burned (WBP) and Weston unburned (WUP) prairie measured at four levels of irradiance in 1995. Values are means \pm one standard error.

RESULTS

Phenology

The slopes of the RLDS were significantly ($P < 0.017$) different among PS ($Y = 2.25 + 7.4X, r^2 = 0.93$), WBP ($Y = 2.34 + 7.1X, r^2 = 0.92$), and WUP ($Y = 8.01 + 6.6X, r^2 = 0.85$). The PS plants completed leaf expansion and senescence in 92 days, four days and five days fewer than WBP and WUP, respectively.

Photosynthesis

On each sampling date in 1994 and 1995, there were no significant differences between sites for the environmental conditions, stomatal conductance, or transpiration rates (data available upon request). On 12-17 May 1994, PP plants had significantly ($P < 0.05$) higher photosynthetic rates than PS plants at 100%, 50%, and 10%

Table 1. Shooting star leaf morphology for ParkLands Savanna and Weston Prairie (burned and unburned) during the 1995 season. Values are population means \pm 1 SE.

	(n)	ParkLands Savanna	Weston Prairie Burned	Weston Prairie Unburned
Surface Area (cm ²)*	15	23.5 \pm 2.6a	27.4 \pm 3.2a	27.9 \pm 2.5a
Length:Width	15	3.74 \pm 0.18a	3.21 \pm 0.14b	4.87 \pm 0.17c
Thickness (mm)	10	0.56 \pm 0.02a	0.67 \pm 0.04b	0.50 \pm 0.02a
Stomatal Densities (number/cm ²)				
Lower Epidermis	15	15.5 \pm 0.3a	16.4 \pm 0.3a	13.6 \pm 0.2b
Upper Epidermis	15	13.6 \pm 0.3a	14.8 \pm 0.2b	12.8 \pm 0.3c
Total Leaf Surface	15	29.2 \pm 0.5a	31.2 \pm 0.5b	25.4 \pm 0.4c
Leaf Mass per Area mgcm ⁻²	16	4.5 \pm 0.1a	5.4 \pm 0.2b	5.1 \pm 0.2b

* For each row, means followed by the same letter are not significantly different ($P < 0.05$), Tukey HSD mean separation procedure.

irradiance of full sunlight, and approached significance ($P = 0.06$) at the 25% levels (Fig. 1). For 27–29 May 1994, there were significant ($P < 0.05$) site by shade interactions, with the PS plants having higher photosynthetic rates at 100% full irradiance than PP plants (Fig. 1).

On 5 May 1995, there were significant ($P < 0.01$) differences in photosynthetic rates owing to site by shade interactions with plants from WBP having higher rates of photosynthesis than plants from PS and WUP under 100% and 50% full irradiance (Fig. 2). Under the 25% light level, WBP plants had higher photosynthetic rates than plants from WUP. On 15 May 1995, there were significant ($P < 0.001$) site by shade interactions with WBP plants having higher photosynthetic rates than plants from PS under 100% full irradiance (Fig. 2). There were no differences in photosynthetic rates among sites for the 21 May 1995 sampling. Maximum rates of photosynthesis during May were higher for WBP ($20.6 \pm 0.6 \mu\text{mol/m}^2/\text{s}$) than for WUP (12.0 ± 0.2) or PS (13.8 ± 0.2) plants (Fig. 2).

Leaf Morphology

Mean leaf area per plant did not differ significantly ($P = 0.16$) among sites; however, the leaf length to width ratios were significantly ($P < 0.05$) different. Plants from WBP had the largest ratio followed by PS and WUP plants. Leaves from WBP were significantly ($P < 0.001$) thicker than those of PS and WUP plants (Table 1). Total and upper epidermal stomatal densities were significantly ($P < 0.001$ for both) different among plants from all three sites. The WBP plants had the highest densities, followed by PS and WUP plants (Table 1). The PS plants had significantly ($P < 0.05$) lower leaf mass per area than WBP and WUP plants (Table 1).

DISCUSSION

Spring ephemerals, like shooting star, grow and set seed before the dominant vegetation becomes active (Knapp 1986). In prairie or savanna, it would be advantageous for a short statured ephemeral plant to complete its advent growth before being shaded by the dominant vegetation. The rates of phenological development (RLDS) were statistically different between the savanna and prairie plants, supporting our prediction. However, the actual differences between savanna and prairie plants were relatively small with the savanna plants completing their seasonal growth in four to five days earlier than the prairie plants. This suggested that plants in the savanna and prairies habitats may be under similar selection pressure to complete their leaf development and senescence cycle before the dominant vegetation shades them. The savanna tree canopy is fully de-

veloped by mid to late May, whereas the prairie canopy does not reach maximum height or density until late in the summer. The grasses are actively growing by late April and are shading the basal rosettes of shooting stars a few weeks after they begin growth. Consequently, seasonal patterns of shading are similar in the two habitats for plants with basal rosettes.

Plants from the burned prairie had higher photosynthetic rates than savanna plants at the two highest levels of irradiance in early May, as we expected. There were no significant differences in photosynthetic rates among plants from the three sites in late May. Savanna plants retained a relatively consistent rate of photosynthesis throughout the period when measurements were made, whereas plants from the burned prairies had high rates of photosynthesis early in the growing season but these rates declined later.

Weston Prairie shooting star plants responded positively to the full irradiance conditions that occurred on the burned portion of the prairie early in the growing season. Plants on the burned prairie had higher photosynthetic rates than plants on the unburned prairie early in the growth season; however, these differences diminished as the dominant prairie grasses began to develop a canopy over the shooting stars. This decrease in photosynthesis, as the grasses alter the plant level environmental conditions, was consistent with studies of other prairie species (Knapp 1984, Knapp 1985, Knapp and Seastedt 1986, Collins and Wallace 1990, Glenn-Lewin et al. 1990).

The differences in photosynthetic rates between plants grown in burned savanna and burned prairie appear to be associated with habitat effects. Plants growing in the savanna had relatively consistent carbon assimilation rates throughout the season, while plants growing in the burned prairie had high carbon assimilation rates. The differences in photosynthetic rates between prairie and savanna plants decreased as the season progressed.

Differences in the leaf morphology were largely related to level of PPFD under which the plants developed, regardless of habitat. At the beginning of the growing season, WUP plants had the lowest irradiance, followed by plants in the PS and WBP. In the unburned prairie (WUP), leaves began development in dense, compact litter from the previous season and experienced low levels of incident radiation. However, even after shoots emerge above the litter, incident PPFD available to shoots in an undisturbed tallgrass prairie early in the growing season may be as much as 58% lower within standing vegetation compared to above canopy levels (Knapp 1984, Knapp and Gilliam 1985). Accordingly, we found the retention of several leaf morphological and physiological characteristics of shade leaves for plants growing in the unburned prairie, which is congruent with the results of Knapp and Seastedt (1986).

Plants in the burned savanna and the unburned prairie had similar morphology and photosynthetic rates. This suggested that partial shading in the savanna habitat from tree trunks and branches could have been responsible for the reduced photosynthetic rates early in the growing season. The results of this study suggested that phenological development, photosynthetic rate, and leaf morphology responses of shooting star plants were related to the seasonal dynamics of the dominant vegetation and the effect of burning that altered irradiance regimes on burned prairies. In the absence of reciprocal transplant experiments between savanna and prairie habitats, we can not be sure that genetic differences between populations are not at least partially responsible for the morphological and physiological differences.

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Genetic Variation Among Remnant Iowa Populations of Rough Blazing Star (*Liatris aspera* Michx.)

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Increasing efforts to conserve and restore tallgrass prairie have resulted in a large demand for seed of native prairie plant species. Conservation and restoration practitioners have recognized the potential importance of utilizing seed with 'locally adapted' genotypes, but little information is available on the degree and geographic distribution of genetic variation for most prairie plant species. Rough blazing star (*Liatris aspera* Michx.) is one species that is included in the Iowa Ecotype Project, an effort to provide readily available seed of native prairie plants that is produced in a manner that aims to conserve the genetic integrity of local populations and maximize genetic variability in the seed stock. We used random amplification of polymorphic DNA (RAPD) to assess the pattern of genetic variation among six remnant populations of *L. aspera* in Iowa and examined geographic distance between populations as a potential factor in explaining the patterns of variation revealed by RAPD. Results indicate that 78% of variability occurs within populations while 22% of the variation is due to differences between populations. No significant relationship was found between observed patterns of genetic similarity and geographic proximity. Though based on a small number of populations and relatively few samples, these findings suggest a conservation strategy for *L. aspera* in Iowa that emphasizes collecting seed from a greater number of individuals rather than maximizing the number of populations.

INDEX DESCRIPTORS: *Liatris aspera*, ecotype, genetic variation, prairie, RAPD.

Rough blazing star (*Liatris aspera* Michx.) is a native, outcrossing, perennial prairie forb that is common throughout the tallgrass prairie. In Iowa, as in other parts of the tallgrass prairie region, nearly all the historic tallgrass prairie has been converted to agriculture (Risser 1988). Of the original 12.5 million ha, the less than 0.1% that remains occurs as isolated remnants ranging in size from fractions of a hectare to about 100 ha at the largest (Samson and Knopf 1994). Interest in conserving, restoring, and reconstructing prairies began in the 1930s (Curtis 1952, Blewett and Cottam 1984) and has steadily increased since the 1960s (Shirley 1994). Because of the high cost and limited availability of locally collected seed, commercially produced native prairie plant seed has been increasingly used in restoration and reconstruction efforts (Smith 1994, Knapp and Rice 1996). With widespread use of these cultivated varieties, concern has arisen over the conservation of genetic integrity of extant populations and the adaptability of these strains to particular local environments (Millar and Libby 1989, Knapp and Rice 1994). Frequently, the response to this concern has been insistence on the use of only locally collected seed. While this ensures that 'alien' genetic material will not be introduced, it confines the area from which seed is collected and potentially limits the genetic variability of collections. In addition, a low initial level of genetic variability could be exacerbated in a small planting by loss of genetic characters through random genetic drift and limited gene flow, resulting in even lower genetic variability (Young et al. 1996). The Iowa Ecotype Project has been developed in response to these concerns regarding the source of seed to be used for prairie plantings in Iowa.

The Iowa Ecotype Project is an effort to provide seed of native prairie plant species that is readily available, affordable, and is pro-

duced in a manner that aims to conserve the genetic integrity of local populations and maximize overall genetic variability in the seed stock. An 'ecotype' is a genetically differentiated strain of a species that is adapted to a specific set of environmental conditions and is restricted to habitats in which those conditions prevail (Smith 1994). The ecotype concept was first introduced in the 1920s following research conducted with multiple plant species over several years (Turesson 1922, 1925). In North America, the work of Clausen, Keck and Hiesey (1940, 1948) and Clausen and Hiesey (1958) in the western United States, and later McMillan (1959a, b, 1964, 1965a, b) in the tallgrass prairie region, served to solidify the ecotype concept and further clarify the importance of patterns of genetic variation within plant species.

The primary goal of the Iowa Ecotype Project is to propagate ecotypes of 20–25 species of grasses and forbs while maintaining or enhancing the genetic variability existing in these species. Three ecotype collections for each species are established based on the division of the state into three zones, each consisting of three latitudinal tiers of counties (Fig. 1). The project was originally designed to include more zones, but concerns over marketability of seed in a small area led to the decision to have only three. Ecotype collections are developed by harvesting seed randomly from several (10 or more) remnant populations in each of the three zones, pooling all seed by zone, and increasing the volume of seed by cultivating it in plots located on the University of Northern Iowa campus in Cedar Falls, Iowa and at the USDA Plant Materials Center in Elsberry, Missouri. There is no intentional selection for particular traits during the harvesting or cultivation process, so maximum variability is preserved in each collection. One of the species that has been selected for the Ecotype Project is *Liatris aspera* Michx. (rough blazing star), and it is the existing genetic variation of extant populations of this species in Iowa that is the focus of the research presented here. To conserve

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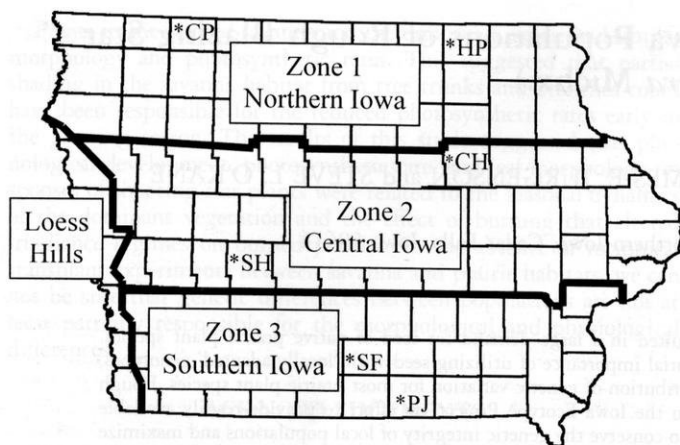


Fig. 1. Iowa Ecotype Project zones and locations where *Liatris aspera* populations were sampled. The Loess Hills area of western Iowa was excluded from the first phase of the Iowa Ecotype Project due to a dramatically different floral composition as compared to the remainder of the state. (CP = Cayler Prairie, HP = Hayden Prairie, CH = Cedar Hills Sand Prairie, SH = Sheeder Prairie, PJ = Plano-Jerome roadside, SF = Stephen's Forest roadside).

genetic variability efficiently and effectively, it is necessary to first obtain information regarding how much existing variability there is. Additionally, it is imperative to have some knowledge of how the variation is distributed across the geographic range of interest. Once this has been established, sampling strategies can be devised to conserve a maximum of the existing variability in the most efficient and cost-effective manner.

The goal of this research was to use random amplified polymorphic DNA (RAPD) to assess the degree and pattern of genetic variability of six remnant populations of *Liatris aspera* in Iowa. The RAPD method has been shown to be able to detect polymorphisms at both the intra-specific and intra-population levels (Welsh and McClelland 1990, Hedrick 1992). RAPD markers were successfully used to detect genetic variability in a variety of plant taxa including spruce (van de Ven and McNicol 1995, Bucci and Menozzi 1995), pine (Lu et al. 1995, Plomion et al. 1995), cocoa (Wilde et al. 1992, Russell et al. 1993), corn (Heun and Helentjaris 1993), and several native prairie grasses (Huff et al. 1993, Gunter et al. 1996, Huff et al. 1998, Gustafson et al. 1999).

An important assumption that is implicit in many conservation, restoration, and reconstruction efforts where there are "local ecotype" concerns is that there exists a positive relationship between the geographic proximity of seed or other plant material sources and the genetic similarity of these materials. While some studies have shown genetic structuring among natural populations (Godt and Hamrick 1996, Castagne et al. 1997, Demissie et al. 1998), other researchers have reported no relationship between genetic and geographic distance among populations at the landscape scale (Knapp and Rice 1996, Huff et al. 1998, Gustafson et al. 1999). By examining the relationship of geographic nearness and indices of RAPD similarity between the sampled populations of *L. aspera*, the hypothesis of a positive correlation between these two metrics can be explicitly tested. Our specific objectives were (1) to characterize the level of inter- and intra-population genetic variability, (2) to examine geographic distance as a potential factor in explaining the patterns of variability revealed by RAPD, and (3) to discuss the results of these analyses as they relate to the current sampling strategy of the Iowa Ecotype Project.

METHODS

Study sites

Two remnant prairies from each of the three Iowa Ecotype Project zones were sampled for this study (Fig. 1). All field sampling was completed 6–8 September 1996, at which time *L. aspera* was abundant at all sites, although no formal census was conducted. Following are descriptions of the sites where each of the six populations of *L. aspera* was found. Included in the descriptions are the two-letter codes that are used to refer to each population throughout this paper (e.g. CH for Cedar Hills Sand Prairie) and the approximate Universal Transverse Mercator (UTM) coordinates for the sites (UTM Zone 15, NAD 27), which were used to determine geographic distances between the populations.

Zone 1—Northern Iowa. Cayler Prairie State Preserve (CP; UTM 318173, 4806983) is located approximately 10 km northwest of Wahpeton in northwest Dickinson Co. This 65 ha site has been managed by the Iowa Department of Natural Resources (IDNR) since its dedication in 1971 and is characterized by shallow, rocky soils on ridges interspersed with wet swales resulting from erosion of the remnant glacial moraine. Hayden Prairie State Preserve (HP; UTM 550151, 4809034) is a 97 ha black-soil prairie located approximately 7.2 km north of Saratoga in Howard Co. With community types ranging from mesic to wet, this high quality remnant was preserved in 1948 by the IDNR and later named in honor of Iowa prairie researcher Dr. Ada Hayden.

Zone 2—Central Iowa. Cedar Hills Sand Prairie (CH; UTM 537440, 4717071) is located just south of Finchford in extreme northwestern Black Hawk Co. and is managed by The Nature Conservancy. This 14 ha site was dedicated in 1985 and is characterized by very sandy soils of eolian origin with community types ranging from wet prairie fen to dry sand prairie. Sheeder Prairie State Preserve (SH; UTM 363399, 4615275) is a 10 ha preserve located about 4 miles west of Guthrie Center in Guthrie Co. This mesic prairie remnant was dedicated in 1968 and is managed by the IDNR.

Zone 3—Southern Iowa. Plano-Jerome (PJ; UTM 496062, 4510146) roadside remnant is located between the towns of Plano and Jerome in Appanoose Co. Though not officially managed, this species-rich remnant of slightly less than 5 ha appeared to have been hayed prior to the time of tissue collection. Stephens Forest (SF; UTM 461520, 4538806) is another roadside prairie remnant smaller than 5 ha found about 6.5 km south of the town of Lucas in Lucas Co.

Population sampling

At each site, sections of fresh, mature leaf tissue were obtained from 30 plants using a randomly stratified sampling procedure (ultimately, only 10 randomly chosen individuals from each population were used in the RAPD analysis due to time and resource constraints). To minimize the possibility of taking multiple samples from a single plant clone, only plants that were at least three m apart were sampled. Care was taken to avoid obviously damaged or potentially infected sections based on visual inspection. Multiple (2–4) samples were taken from each plant by pinching off a 3–4 cm long section of tissue between the lid and opening of a 1.5 ml microcentrifuge tube. The number of sections taken was based primarily on the width of the leaf so that a total of approximately 400 mg of tissue was obtained from each plant. The tubes had been previously autoclaved and partially filled with silica gel as a desiccant. All sample tubes were packaged in Ziploc® bags and placed on ice until they could be frozen at -75°C .

Isolation of genomic DNA

Isolation of total genomic DNA for RAPD templates followed the modified CTAB protocol of Doyle and Doyle (1987) as described by Kitchen (1999). Template DNA stock concentrations were determined using A_{260} values (1 O.D. = 50 ng/ μ l) obtained with a Beckman® Acta™ III spectrophotometer (Beckman Instruments). Aliquots of each template stock were diluted to a concentration of about 20 ng/ μ l, and each template dilution was divided into 20 μ l aliquots and stored at -75°C .

RAPD profiling

Twenty decamer primers from Operon® Kit A (Operon Technologies) were screened for the ability to generate reproducible banding patterns. Only bands that were reproducible were included in the analysis. A band was considered to be reproducible if it appeared in two or more separate amplifications for a particular primer/template combination. Bands were scored as present or absent based on repeated amplifications for each primer/template combination. A total of 11 primers (5' to 3' sequence and number of bands scored follows in parentheses) were used in the analysis: A-01 (CAGGCCCTTC, 14), A-02 (TGCCGAGCTG, 21), A-03 (AGTCAGCCAC, 19), A-04 (AATCGGGCTG, 22), A-05 (AGGGGTCTTG, 21), A-07 (GAAACGGGTG, 15), A-08 (GTGACGTAGG, 16), A-09 (GGGTAACGCC, 19), A-10 (GTGATCGCAG, 24), A-12 (TCGGCGATAG, 23), A-19 (CAAACGTCGG, 17). RAPD amplifications were run in sets of 30 plus one blank. Each set consisted of a single reaction for each of 10 individuals from three populations. Procedures for RAPD cycling and agarose gel electrophoresis were as described by Kitchen (1999). Gel images were captured with a BioImaging Technologies video image capturing system and recorded using NIH Image software v.1.51 (National Institutes of Health, USA) on an Apple Macintosh® Quadra 840AV™ computer. Gel images were analyzed with GelReader software (v. 2.0.4 National Center for Supercomputing Applications 1991) using two molecular weight standards, a *Hind* III restriction digest of lambda DNA and a *Hinf* I digest of plasmid Bluescript+KS, to estimate the sizes of RAPD fragments.

Data analysis

The proportion of bands unique to an individual population was calculated for all possible comparisons of 2, 3, 4, 5, and 6 populations according to Yu and Pauls (1993):

$$F_{(n)} = \frac{\sum_{i=0}^{n-2} (n-i)c_{i,\dots,n}^{(n-i)}}{\sum_{a=1}^n X_a}$$

where n is the number of populations being compared, $i = 0, \dots, (n-2)$, $c_{i,\dots,n}^{(n-i)}$ is the number of common bands in all possible comparisons of n populations in $(n-i)$ groups [note $(n-i)$ is not an exponent], X_a is the total number of bands per population, and $a = 1, \dots, n$. The analysis of population-specific bands is of interest in this study because it provides some indication of the probability of encountering novel genetic characters as additional populations are sampled. This information is useful in that it can be used to evaluate the effectiveness of the sampling strategy employed in the Iowa Ecotype Project in meeting the goal of maximizing genetic variability in the Ecotype collections of *L. aspera*.

The degree of genetic variability within populations was assessed by making pair-wise comparisons of the RAPD profiles of all individuals in each population (total of 10 individuals per population,

45 total comparisons per population) (Kresovich et al. 1992). For each population, genetic similarity of individuals was calculated (Nei and Li 1979):

$$\text{Similarity (F)} = (2N_{ab})/(N_a + N_b)$$

where N_{ab} is the number of shared fragments between individuals 'a' and 'b', N_a is the total number of fragments scored for all primers for individual 'a', and N_b is the total number of fragments scored for all primers for individual 'b'. Within-population similarity (F_w) values are reported for each population and are the mean of all F values for all pair-wise comparisons of individuals in that population.

Genetic similarity between populations (F_b) was calculated using the same equation as above, except that in the equation for genetic similarity, the variables N_{ab} , N_a , and N_b refer to entire populations rather than individuals (Yu and Pauls 1993). The values of F_b were calculated for all pair-wise comparisons of populations (total of 6 populations, 15 pair-wise comparisons). A second index of genetic variability between populations was calculated which takes the frequency of occurrence of each RAPD band in the populations into account (Yu and Pauls 1993). As a measure of similarity, the genetic identity index (GII) was calculated:

$$\text{GII} = \frac{1}{N} \sum_{i=1}^N \frac{2V_i^{(1)} \cdot V_i^{(2)}}{[V_i^{(1)}]^2 + [V_i^{(2)}]^2}$$

where N is the total number of fragments scored for all primers in the two populations being compared, and $V_i^{(1)}$ and $V_i^{(2)}$ are the frequency of occurrence of an individual band i in populations 1 and 2, respectively.

For each primer used, the diversity of RAPD bands was apportioned within and among populations using Shannon's information measure (Lewontin 1972):

$$H_o = -\sum p_i \ln_2 p_i$$

where p_i is the frequency of a polymorphic band when present. H was calculated for two levels of RAPD band frequency, following King and Schaal (1989): where H_{pop} is the average diversity within populations, and H_{sp} is the diversity within species. The proportion of diversity within populations was H_{pop}/H_{sp} , and the proportion of diversity among populations was $(H_{sp} - H_{pop})/H_{sp}$. The overall partitioning of RAPD variability was determined by calculating means of total, within-population, and among-population variability across all primers.

To illustrate the phenetic relationships of all individuals of *L. aspera* revealed by RAPD analysis, two methods were employed. First, a minimum evolution tree was generated using PAUP* software (v.4, Swofford 1999) and the RAPD band data. An unrooted tree was used because there was no information regarding a potential "origin" population or individual. The tree was generated with Heuristic Search, MAXTREE, and TBR branch swapping options selected. Second, a principle components analysis (PCA) was performed on the RAPD band presence/absence data using the PRINCOMP procedure of SAS (v6.12, SAS Institute Inc. 1996), and the results of the PCA were used to make a 3-D plot of individuals based on the first three principle components.

To test the hypothesis that there is a relationship between the geographic proximity and genetic similarity of these populations (ie. landscape-scale genetic structure), the Mantel program of Liedloff (version 2.0 1999) was used to evaluate associations between geographic distance and both indices of similarity, F_b and GII, using the Mantel test (Mantel 1967).

RESULTS

All 11 primers that were used in the analysis generated bands that detected variability both within and between populations. The num-

Table 1. Percentage of population-specific bands in comparisons of 2, 3, 4, 5, or 6 populations of *L. aspera*. Values represent the mean of all possible comparisons of *n* populations.

# of Populations Being Compared	% of Population Specific Bands
2	14.07
3	5.18
4	2.85
5	1.89
6	1.38

number of polymorphic loci detected varied between primers, ranging from 14 for primer A-01 to 24 for primer A-10, with a total of 211 bands used to evaluate genetic variability within and among the six remnant populations. Only 14 of the bands scored were unique to a single population. Overall, the average percentage of bands that were population-specific was only about 14% when any two populations were compared, and less than 1.5% of the bands were population-specific when all six populations were included in the comparison (Table 1).

Estimates of similarity between populations (F_b) ranged from 0.8348 for CH compared to SH and a maximum of 0.8775 for the comparison of CP to PJ. Estimated similarity (F_w) between individuals in a single population was much lower than that between populations, with the lowest average similarity of individuals of 0.4745 in population HP and the greatest average F_w of 0.5322 in population CH (Table 2). The populations that were least similar based on the genetic identity index (GII) were CH and SH, with a value of 0.5677, and CP and HP were most similar with $GII = 0.6583$ (Table 3). The GII differs from F_b in that the GII takes both the number and frequency of occurrence of shared bands into account. The rank-order of population similarity changed somewhat when this element of genetic structure (frequency of alleles) was included in

the analysis (e.g., CP-PJ ranked most similar based on F_b , while this pair ranked eighth most similar when GII was calculated), but the overall range of between-population similarity values was small regardless of which index was used.

A visual representation of the genetic relatedness of the 60 individuals of *L. aspera* included in the study is presented in a minimum evolution tree that was generated using PAUP* software (v. 4, Swoford 1999) and RAPD band presence/absence data (Fig. 2). Relationships identified by the tree are similar to those described by the genetic identity index (GII) at the population level. Examination of the tree reveals what appear to be four distinct groups, each comprised of individuals from two or more populations. Individuals from the CP population are clustered into two separate groups, one each with individuals from populations HP and CH (GII rank #1 and #2 of 15, respectively), individuals from the SH population are grouped with those from the SF population (GII rank #4), and there is one group comprised primarily of individuals from populations PJ and SF (GII rank #6). The short branch lengths between the four groups as compared to the relatively long branches between individuals indicate that the genetic differentiation between groups is weak and that most of the variability is between individuals within groups.

A principle components analysis was performed using SAS software (v.6.12, SAS Institute 1996) and the RAPD band data to further evaluate the relationships of the individuals in the study. A 3D plot of the first three principle components illustrates the nature of the relationships detected by the principle components analysis (Fig. 3). This figure corroborates the pattern of individual-level relationships suggested by the minimum evolution tree (e.g., note the clustering of individuals 42, 43, 44) but allows discrimination of 'distance' between individuals that could not be illustrated in the two-dimensional tree (e.g., individuals 35, 12, and 11 are adjacent in the tree, but the PCA plot clearly shows that individuals 11 and 35 are more similar to one another than to individual 12 when the third dimension is considered). As with the minimum evolution tree, there appears to be some clustering of individuals, but it is weak at best.

The Shannon information measure was used to apportion diversity

Table 2. Similarity matrix generated from Nei and Li's (1979) estimate of similarity based on the number of shared bands. Values on the main diagonal are mean values of within-population similarity (F_w) based on all pair-wise comparisons of individuals ($n = 10$) in that population. Values below the diagonal are between-population similarity (F_b).

Population	CP	HP	CH	SH	PJ	SF
CP	0.5177					
HP	0.8772	0.4745				
CH	0.8728	0.8554	0.5322			
SH	0.8513	0.8571	0.8348	0.5211		
PJ	0.8775	0.8487	0.8504	0.8639	0.5276	
SF	0.8522	0.8701	0.8537	0.8614	0.8588	0.4811

Table 3. Genetic identity index (GII) (Yu and Pauls 1993) matrix based on a comparison of the number and frequency of occurrence of bands between six populations of *L. aspera*. Values of ' GII ' indicate the level of genetic similarity between populations.

Population	CP	HP	CH	SH	PJ	SF
CP	1.0000					
HP	0.6583	1.0000				
CH	0.6322	0.5967	1.0000			
SH	0.5871	0.6105	0.5677	1.0000		
PJ	0.6103	0.5962	0.5895	0.6174	1.0000	
SF	0.5863	0.6290	0.5936	0.6280	0.6130	1.0000

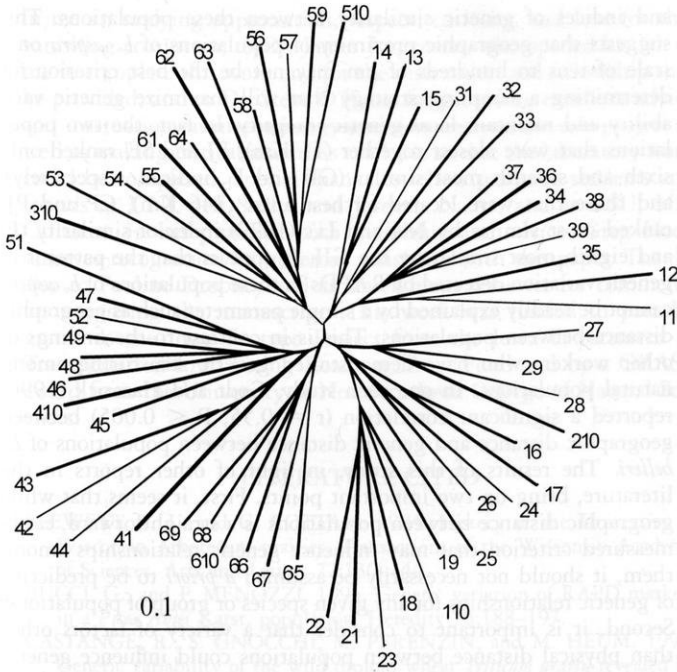


Fig. 2. Minimum evolution tree indicating relationships of individuals of *L. aspera* based on RAPD data. Branch lengths indicate number of evolutionary steps necessary for observed variability in RAPD genotype (bar = 0.1 steps). Code numbers of individuals are as follows: first digit refers to population (1 = CP, 2 = HP, 3 = CH, 4 = SH, 5 = PJ, 6 = SF), second (and third) digits refer to the number of the individual from the population (e.g., '510' refers to population 5 (PJ), individual number 10). The tree was generated using RAPD band data and PAUP software to generate an unrooted tree with Heuristic Search, MAXTREE, and TBR branch swapping options selected.

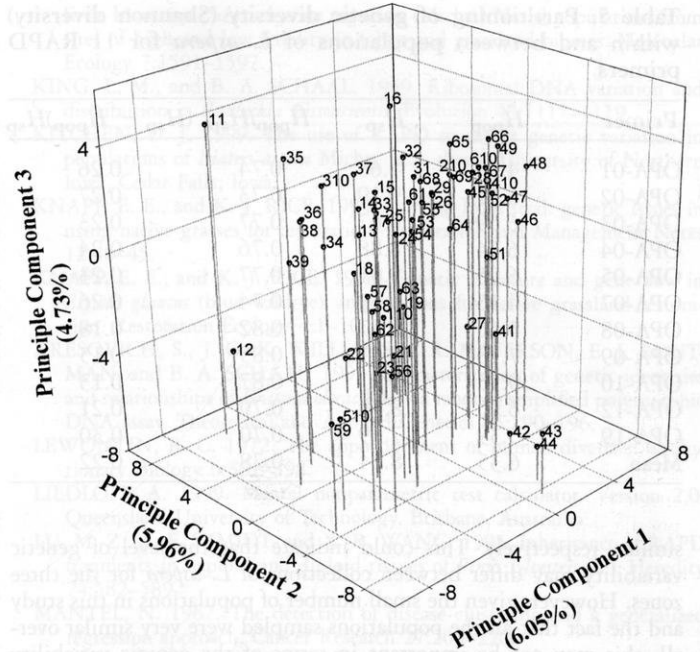


Fig. 3. 3D plot of the first three principle components describing the variability between individuals of *L. aspera*. Values in parentheses indicate the proportion of the total variation explained by each component (note: it required 28 principle components to describe 75% of the variation in the sampled individuals). Code numbers for individuals are as described in Fig. 2.

into within- and between-population components. Estimates of diversity (H_o) were calculated based on each primer for each population (Table 4). The greatest average diversity was detected in the CP population ($H_o = 6.67$) while the CH population had the least diversity ($H_o = 6.10$) on average. Different primers detected varying levels and rank-orders of diversity between populations (e.g., SF was most diverse and CH least diverse with respect to primer OPA-01, while CH ranked most diverse and SF ranked fourth in diversity when primer OPA-02 was used). Values of population diversity varied across a range of 3.02 for primer OPA-07 and population SH to 11.09 for primer OPA-10 and population SF.

Average Shannon diversity within populations (\bar{H}_{pop}) was 6.35, with a range of 4.16 detected by primer OPA-07 to 9.55 detected by primer OPA-10. Overall diversity (H_{sp}) within *L. aspera* was 8.14, ranging from 5.62 to 11.01 as detected by primers OPA-07 and OPA-10, respectively. The proportion of overall diversity present within populations (\bar{H}_{pop}/H_{sp}) ranged from 0.70 (primer OPA-19) to 0.87 (primer OPA-10) and averaged 0.78. The proportion of diversity attributed to variability between populations ($(H_{sp} - \bar{H}_{pop})/H_{sp}$) ranged from 0.13 to 0.30 with an average of 0.22 (Table 5). The results of the Mantel tests indicated no significant association between geographic distance and genetic similarity by either F_b ($Z = 0.21, P = 0.23$) or GII ($Z = -0.002, P = 0.49$).

DISCUSSION

The RAPD method successfully detected genetic variability both within and between six populations of *L. aspera* Michx. in Iowa using

Table 4. Estimates of genetic diversity (H_o) within six populations of *L. aspera* for each of 11 primers.

Primer	Population					
	CP	HP	CH	SH	PJ	SF
OPA-01	3.86	4.77	3.06	5.12	3.30	5.28
OPA-02	7.07	5.33	7.66	7.39	6.25	6.57
OPA-03	6.13	6.46	6.16	6.76	6.84	7.79
OPA-04	7.27	6.39	6.35	7.16	6.56	6.68
OPA-05	8.08	7.24	6.30	5.66	8.24	6.17
OPA-07	3.82	5.59	5.02	3.02	3.54	3.97
OPA-08	6.77	5.43	5.15	4.78	5.07	5.18
OPA-09	7.90	7.01	7.71	7.49	6.38	6.29
OPA-10	7.98	9.70	9.97	9.91	8.65	11.09
OPA-12	7.89	6.72	4.57	7.85	9.02	5.68
OPA-19	6.60	5.09	5.15	4.29	6.78	4.43
Mean	6.67	6.34	6.10	6.31	6.42	6.28

11 decamer primers. Of the 211 polymorphic bands scored, only 14 were unique to a single population. Similarity values were higher when calculated based only on the number of shared bands than when both the number and frequency of shared bands were included in the calculation. Overall, the rank-order of similarity of population pairs was different between the two indices of similarity, but the rank-order of similarity of population pairs within an ecotype zone varied little. In Zone 1, the CP-HP pair ranked #2 and #1 (of 15) by Nei and Li's (1979) similarity ' F_b ' and the genetic identity index ' GII ', respectively, while in Zone 2, the rank of CH-SH similarity was #15 by both indices. In Zone 3, PJ-SF ranked #7 and #6 most

Table 5. Partitioning of genetic diversity (Shannon diversity) within and between populations of *L. aspera* for 11 RAPD primers.

Primer	\bar{H}_{pop}	H_{sp}	$\bar{H}_{\text{pop}}/H_{\text{sp}}$	$(H_{\text{sp}} - \bar{H}_{\text{pop}})H_{\text{sp}}$
OPA-01	4.23	5.68	0.74	0.26
OPA-02	6.71	9.19	0.73	0.27
OPA-03	6.69	8.67	0.77	0.23
OPA-04	6.74	8.88	0.76	0.24
OPA-05	6.95	9.05	0.77	0.23
OPA-07	4.16	5.62	0.74	0.26
OPA-08	5.40	6.57	0.82	0.18
OPA-09	7.13	8.41	0.85	0.15
OPA-10	9.55	11.01	0.87	0.13
OPA-12	6.95	8.79	0.79	0.21
OPA-19	5.39	7.69	0.70	0.30
Mean	6.35	8.14	0.78	0.22

similar, respectively. This could indicate that the level of genetic variability may differ between collections of *L. aspera* for the three zones. However, given the small number of populations in this study and the fact that all the populations sampled were very similar overall, this may not be important in terms of the genetic variability within the Ecotype collections as a whole for this species. Average diversity between individuals within populations was greater than that between populations. A similar finding was reported by Dolan et al. (1999) in their study of rare Florida scrub endemics, with very little differentiation among 30 populations of *Liatris oblongerae* (average similarity of 0.987 based on 12 isozyme loci), while *L. oblongerae* had the highest overall levels of genetic variation among the three species studied. For *L. aspera* in this study, the Shannon information measure indicated that on average, 78% of the total variability within the sample was found within populations, while an average of 22% of the genetic variability was attributed to the between-population component. Godt and Hamrick (1996) reported that 16% of allozyme diversity could be attributed to among-population differences in *Liatris helleri*, a federally listed congener. Levels of population differentiation in this range (0.15 to 0.25) have been described as "indicating moderately great differentiation" (Wright 1978). These measures of genetic variability taken together strongly indicate that the greatest amount of variability in the sample of *L. aspera* that was evaluated is due to differences of individuals within populations rather than between populations as a whole. However, differences between populations appear to be considerable and should not be overlooked. This suggests that with respect to the goal of maximizing genetic variability of seed collections, the effort to sample *L. aspera* in Iowa should be concentrated on maximizing the number of individuals that seed is collected from within populations and that the total number of populations that are sampled does not necessarily need to be large. The number of novel genetic characters that would be acquired by sampling additional populations (there are currently 10+ populations sampled in each zone) is probably very low, as evidenced by the analysis of population-specific bands (Table 1).

The minimum evolution tree (Fig. 2) and the plot of the principle components (Fig. 3) illustrate that while there is some clustering of populations, these groups are not strongly differentiated, and when these figures are reviewed in the context of the geographical variation represented by the locations of the six populations, there is no clear pattern to the genetic relatedness of the populations or individuals. This conclusion is further supported by the results of the Mantel tests, where no association was found between geographic distance

and indices of genetic similarity between these populations. This suggests that geographic proximity of populations of *L. aspera* on a scale of tens to hundreds of km may not be the best criterion for determining a sampling strategy that will maximize genetic variability and maintain local genetic integrity. In fact, the two populations that were closest together (45 Km), PJ and SF, ranked only sixth and seventh most similar (GII and F_b indices, respectively), and those that were located farthest apart (346 Km), CP and PJ, ranked most similar by Nei and Li's (1979) index of similarity (F) and eighth most similar by the GII. It appears that the patterns of genetic variation detected by RAPDs in these populations of *L. aspera* cannot be readily explained by a simple parameter such as geographic distance between populations. This is in contrast to the findings of other workers who have demonstrated genetic structuring among natural populations. In one such study, Godt and Hamrick (1996) reported a significant correlation ($r = 0.55$, $P < 0.005$) between geographic distance and genetic distance between populations of *L. helleri*. The results of this study, in light of other reports in the literature, bring up two important points. First, it seems that while geographic distance between populations is a straightforward, easily measured criterion that may influence genetic relationships among them, it should not necessarily be assumed *a priori* to be predictive of genetic relationships for any given species or group of populations. Second, it is important to consider that a variety of factors other than physical distance between populations could influence genetic relationships within and among plant populations. This could include climatic and edaphic factors, land management history, the size and time since isolation of remnants/populations, and individual plant life history traits as well as potentially complex interactions between these factors.

The results of this study suggest that the majority of genetic variability of *L. aspera* in Iowa as revealed by RAPD is apportioned within rather than between populations. Because there are few genetic characters that are unique to single populations, the risk of "genetic contamination" resulting from pooling seed collected from a wide range of populations is probably quite low. To maximize genetic variability of seed collections of *L. aspera* for the Iowa Ecotype Project, seed should be collected from the maximum number of individuals in any given population, while the addition of single populations to the sampling effort is not likely to add a large amount of variability to the collection. Because the data suggest that the majority of the variability of *L. aspera* is within rather than between populations and the pattern of this variability cannot be explained by geographic proximity, the current sampling protocol of the Iowa Ecotype Project is probably reasonable with respect to the goals of maximizing variability and conserving local genetic integrity as well as addressing the economic and logistic aspects of collecting, cultivating, and marketing the seed. However, these conclusions are based on data from just six populations of only one of the 20–25 species eventually to be included in the Iowa Ecotype Project. What may be reasonable for conservation of *L. aspera* genetic variability may not be so for other individual species or the Iowa Ecotype Project as a whole. If the sampling strategy is to be further optimized for *L. aspera* and other species with respect to the goals of the Iowa Ecotype Project, more intensive investigations into the mechanisms and factors shaping the patterns of genetic variability of these species will be necessary.

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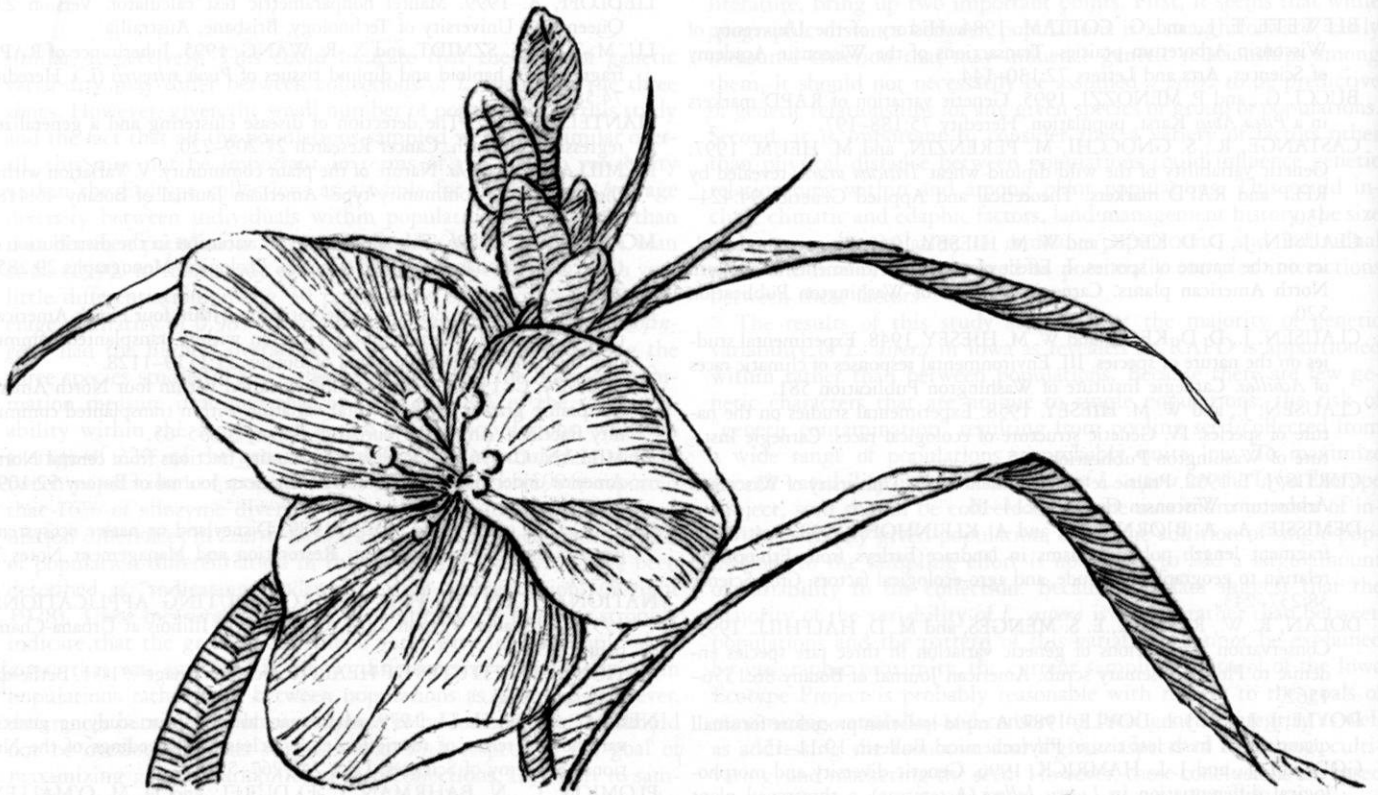
This research was conducted in partial fulfillment of the Master of Arts degree at the University of Northern Iowa. The first author would like to express his deepest gratitude to professor Daryl Smith for introducing me to the world of the tallgrass prairie and instilling

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Patterns of Prairie Plant Species in Illinois Landscape

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Plant species are adapted to specific environmental factors, and, therefore, they are found in different habitats. We used ordination analysis to examine 216 Illinois remnant prairies and determine the major environmental factors influencing Illinois prairie. The prairies separated on the basis of moisture availability, soil texture and topographic position into six types of prairies: dry sand, sand and gravel, hill, "transitional" (dry mesic sand and mesic hill), mesic, and wet mesic/wet. For this study, we examined the relationship between species abundance and ordination group. Average relative frequency values were computed for the major species in each of the six groups. Four of the six types (dry sand prairie, sand and gravel prairies, hill prairies, and the "transitional" prairies) had *Schizachyrium scoparium* (little bluestem) as the leading species with an average relative frequency of 15% or more. Hill prairies also had high abundance of *Bouteloua curtipendula* (side-oats grama grass) and *Sorghastrum nutans* (Indian grass). Although four groups had little bluestem as the leading dominant, historically, it was not the most abundant species in Illinois prairies. Mesic prairies, the most numerous and geographically widespread prairie type in Illinois, had *Andropogon gerardii* (big bluestem) as the species with highest average relative frequency. In wet prairies, *Carex* spp. (sedges) and *Calamagrostis canadensis* (bluejoint grass) were the most common graminoids. Common forbs of the different site-types included *Opuntia humifusa* (prickly-pear cactus) and *Ambrosia psilostachya* (western ragweed) in dry sand prairies, *Dalea purpurea* (purple prairie clover) in hill prairies, and *Aster ericoides* (heath aster) in mesic sites. There was overlap of species along the moisture gradient, demonstrating the continuum of prairie vegetation. These results have potential application to prairie restoration; there is a relationship between topographic position, moisture availability, and species present. This relationship suggests that there are species that should be particularly successful on particular site-types.

INDEX DESCRIPTORS: Illinois prairie, landscape, moisture gradient, species distribution, soil characteristics, vegetation analysis.

A multitude of environmental factors affect the distribution of plant communities on a landscape scale. Sometimes, these factors interact, resulting in complex environmental gradients, which are difficult to measure in the field. By examining the composition of a series of plant communities across space, it is possible to determine what environmental variables are important.

The individualistic model of plant communities (Gleason 1926) states that each plant species has unique environmental requirements. Moreover, the response of some plant species across environmental gradients are known (e.g., see Curtis and Greene 1949, Anderson 1970, Curtis 1971, Umbanhowar 1992, Dhillon and Anderson 1994), so it is possible to interpret the environmental conditions of a site by examining the species present.

Two techniques of data analysis have been developed to compare a series of sites based on the species present. Cluster analysis groups sites or samples into clusters and ordination analysis arranges sites or samples along a continuum. Both techniques use the information about all species present at all sites (and in some cases, the abundances of those species). This information is used to generate a "dissimilarity" measure between all possible pairs of sites based on species presence and abundance. These values are used to arrange the sites into groups or on ordination axes. Because sites with similar species should have environmental similarities, the arrangement of sites should reflect the important environmental factors that affect species composition. Once the analysis has been performed, the researcher can interpret the results and determine which environmental factors are most important.

The major environmental factors affecting plant communities vary with the geographic scale of sampling. On the continental scale,

latitude (as a surrogate for a variety of environmental factors) was the most important variable influencing species composition (Diamond and Smeins 1988), but at smaller scales, moisture availability (Curtis 1971, Nelson and Anderson 1983, Umbanhowar 1992, Corbett 1999) and nutrient availability (Anderson et al. 1984) were the most important factors affecting species composition of prairies. Generally, at the state-to-regional scale, moisture availability is the most important factor affecting prairies.

In a previous study (Corbett 1999, Corbett and Anderson in preparation), we analyzed species abundance data collected for 216 Illinois remnant prairies, originally sampled as part of the Illinois Natural Areas Inventory (INAI) (White 1978). Using detrended correspondence analysis (DCA; Gauch 1982), we determined that there were six groups of Illinois prairies based on soil moisture and soil texture: dry sand prairies, sand and gravel prairies, hill prairies, "transitional" prairies (including dry mesic prairies and some hill prairies), mesic prairies, and wet mesic to wet prairies. This separation did not closely match the six classes of prairie defined by the Illinois Natural Areas Inventory. The six classes the INAI defined were based on substrate (IDENR 1994); we found substrate to be less important than moisture availability. For the current study, we used our six groups of site types as determined by the DCA analysis.

The six prairie groups delineated by DCA analysis differed in soil texture, water availability, and site topographic position. The different groups should have different dominant species. Dominant species differed across different Illinois prairies, for example, Robertson et al. (1997) stated that the four dominant grass species in Illinois were *Andropogon gerardii* Vitman (big bluestem), *Schizachyrium scoparium* Michx. (little bluestem), *Sorghastrum nutans* L. (Indian grass), and

Spartina pectinata Link. (cordgrass). Moreover, Anderson (1970) identified *Andropogon gerardii* as the dominant grass on black-soil prairies, *Spartina pectinata*, *Calamagrostis canadensis* Michx. (bluejoint grass), and *Phragmites australis* Cav. (reed) as the dominant species of wet sites, and *Koeleria cristata* L. (June grass), *Bouteloua curtipendula* Michx. (sideoats grama), and *Bouteloua hirsuta* Lag. (grama grass) as the dominant species of sand prairies (Bazzaz and Parrish 1982). In this paper, we examine the relationship between the general ordination scores of groups of sites and species abundance; in other words, which species seem to be most strongly influencing the ordination assignment.

METHODS

We used data collected from 216 Illinois remnant prairies. The original sampling was done by the INAI in the late 1970s. Sites were selected to be part of the inventory only after they had been ground-truthed and determined by the INAI researchers to be sufficiently undisturbed by human activity (such as grazing, dumping, or heavy recreational use). Prairie sites included in the final survey were sampled for plant species frequency using 20 to 30, 0.25 m² circular quadrats, randomly placed per site (White 1978). Prairie plant frequency data were obtained from the Illinois Department of Energy and Natural Resources in Springfield, Illinois.

Ordination and cluster analyses were performed on the INAI prairie plant data to determine which, if any, environmental gradients affected Illinois prairie. To extract these gradients, we used PC-Ord (McCune and Mefford 1997). After ordination, each of the 216 INAI sites received a series of ordination scores (corresponding to DCA axis 1, 2, and 3 scores). These scores represented the site's position along the environmental gradients: axis 1 represented a moisture gradient and axis 2 separated sites based on topographic position and soil texture.

The INAI remnant prairie data sorted out into six generalized groups in our analyses. These groups differed based on soil moisture, topographic position, and soil texture.

We incorporated the ordination results into a GIS database, using ArcView version 3.1 with Spatial Analyst extension (ESRI 1998). Geographic locations of the INAI sites existed as part of a database produced on CD-ROM by the Illinois Geographic Information System (IDENR 1996). These geographic locations were linked to databases we created that contained information for each of the INAI sites: ordination score, species presence and abundance, and environmental data such as soil association. Thus, it was possible to generate maps and perform spatial analyses on the results of the ordination analyses. To assist with interpretation of ordination results, ordination scores were treated as "spatial data" for some of the analyses. Ordination diagrams were generated in the GIS, where each ordination score was linked to species abundance and environmental data for that site, so ordination diagrams could be produced that showed environmental patterns (for example, Fig. 4).

For this project, we studied the relationship between ordination score and dominant plant species. We separated the sites into six general groups based on ordination axis 1 and 2 score (Corbett 1999, Corbett and Anderson in preparation). We then examined the species composition of the sites in each of the six groups to determine which grass and forb species were dominant in each group. Average relative frequency was calculated for each species in each group of sites.

RESULTS

The DCA ordination separated the 216 INAI sites into six groups (Fig. 1). This separation was largely related to moisture availability, and on the first axis of the ordination, sites were arranged from dry to wet. There was an additional separation among the dry sites on

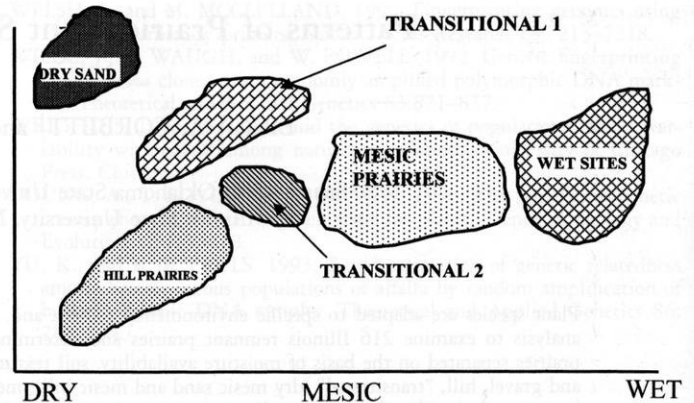


Fig. 1. Site types by group. DCA axes 1 and 2 for analysis of Illinois Natural Areas Inventory sites. On the first ordination axis, sites separate along a moisture gradient from left to right, ranging from dry to wet sites. Six substrate/prairie groups were delineated: (1) dry sand prairie sites in Mason and Henderson counties, (2) transitional sites, including sand and gravel prairies, (3) loess and glacial drift hill prairies, (4) transitional sites including dolomite, loess hill, and dry-mesic prairies, (5) dry-mesic to mesic prairie sites on blacksoil or sand substrates, and (6) wet-mesic and wet sites including wet dolomite sites.

the second ordination axis corresponding to differences in soil texture. Dry sand prairies were separated from hill prairies, which have finer textured soils. Details of this analysis are in Corbett and Anderson (in preparation).

We were able to describe the six groups based on the types of prairies in each group (Table 1). Group 1 contained dry sand prairies; these were sites mostly located on deep Pleistocene sand deposits of west-central Illinois. Group 2 was one of the "transitional" groups found between drier sites and more mesic prairies. Group 2 contained some sand prairies that were not as xeric as the sites located in Group 1, as well as gravel prairies. Group 3 also contained dry prairies, but the sites in this group were loess hill prairies and glacial drift hill prairies. Group 4 was another "transitional" group, located between the hill prairies and more mesic sites. This group contained some hill prairies, dry dolomite prairies, and some dry-mesic prairies. Group 5 was the largest group and contained mesic blacksoil and mesic sand prairies. Group 6 consisted of wet-mesic and wet sites, including several wet dolomite prairies.

The most abundant species, based on relative frequency, for each of these groups are reported in Table 1. In four of the six groups (the dry sand prairies, the hill prairies, and both transitional groups), *Schizachyrium scoparium* was the dominant species. On mesic prairies, *Andropogon gerardii* and *Sorghastrum nutans* were dominant. Finally, wet and wet-mesic prairies had *Carex* spp. as the most abundant graminoid, although the combined relative frequencies of the three leading grasses (*Calamagrostis canadensis*, *Spartina pectinata*, and *Andropogon gerardii*) exceeded that of the sedges.

Each of these four groups also had distinctive species or combinations of species. In addition to having high abundance of *Schizachyrium*, the dry sand sites had *Opuntia humifusa* Raf. (prickly-pear), *Ambrosia psilostachya* DC. (western ragweed), and *Calamovilfa longifolia* (Hook.) Scrib. (sand reed). All of these were species not present in other site types. The hill prairies had high abundance of *Bouteloua curtipendula*, *Sorghastrum nutans*, and *Dalea purpurea* Vent. (purple prairie clover) in addition to the *Schizachyrium*. These species were present in other site-types, but not in combination. The first group of transitional sites (sand and gravel prairies) also had high abundance of *Poa pratensis* L. (Kentucky bluegrass), *Euphorbia corollata* L.

Table 1. Most abundant species of each group of sites. Species having mean relative frequencies of 2 or greater are recorded. Data are given as mean \pm S.E.

Group 1: Dry sand sites. N = 9	
Species	Abundance
<i>Schizachyrium scoparium</i>	16.86 \pm 1.52
<i>Opuntia humifusa</i>	8.44 \pm 1.85
<i>Ambrosia psilostachya</i>	6.72 \pm 2.19
<i>Calamovilfa longifolia</i>	3.86 \pm 1.96
<i>Panicum oligosanthos</i>	3.34 \pm 2.05
<i>Tephrosia virginiana</i>	3.27 \pm 1.68
<i>Bouteloua hirsuta</i>	2.29 \pm 1.53
<i>Stipa spartea</i>	2.04 \pm 1.03
Group 2: Transition between dry sand and more mesic sites N = 6	
<i>Schizachyrium scoparium</i>	17.33 \pm 2.92
<i>Poa pratensis</i>	6.12 \pm 2.36
<i>Euphorbia corollata</i>	5.43 \pm 1.98
<i>Stipa spartea</i>	4.42 \pm 2.39
<i>Echinacea pallida</i>	3.07 \pm 1.95
<i>Lithospermum carolinense</i>	2.70 \pm 2.18
<i>Koeleria cristata</i>	2.52 \pm 1.98
<i>Panicum oligosanthos</i>	2.38 \pm 1.60
<i>Callirhoe triangulata</i>	2.33 \pm 1.65
<i>Dalea purpurea</i>	2.18 \pm 2.18
<i>Tradescantia obtusifolia</i>	2.03 \pm 1.30
Group 3: Hill prairies N = 78	
<i>Schizachyrium scoparium</i>	15.44 \pm 0.65
<i>Bouteloua curtipendula</i>	9.06 \pm 0.80
<i>Sorghastrum nutans</i>	4.53 \pm 0.65
<i>Dalea purpurea</i>	4.50 \pm 0.41
<i>Euphorbia corollata</i>	4.06 \pm 0.45
<i>Echinacea pallida</i>	3.70 \pm 0.46
<i>Solidago nemoralis</i>	3.62 \pm 0.47
<i>Psoralea tenuiflora</i>	2.77 \pm 0.37
<i>Aster azureus</i>	2.46 \pm 0.47
<i>Amorpha canescens</i>	2.34 \pm 0.36
<i>Aster oblongifolius</i>	2.23 \pm 0.47
Group 4: Transition between hill prairies and mesic sites N = 25	
<i>Schizachyrium scoparium</i>	11.55 \pm 1.44
<i>Poa compressa</i>	4.76 \pm 0.93
<i>Euphorbia corollata</i>	4.63 \pm 0.68
<i>Stipa spartea</i>	4.45 \pm 0.99
<i>Bouteloua curtipendula</i>	3.80 \pm 0.81
<i>Amorpha canescens</i>	3.63 \pm 0.73
<i>Echinacea pallida</i>	3.38 \pm 0.61
<i>Sporobolus heterolepis</i>	3.00 \pm 0.63
<i>Rosa caroliniana</i>	2.48 \pm 0.63
<i>Aster ericoides</i>	2.34 \pm 0.61
<i>Commandra richardsoniana</i>	2.07 \pm 0.47
<i>Solidago nemoralis</i>	2.05 \pm 0.63
Group 5: Mesic sites N = 89	
<i>Andropogon gerardii</i>	5.04 \pm 0.51
<i>Sorghastrum nutans</i>	4.37 \pm 0.44
<i>Aster ericoides</i>	3.61 \pm 0.38
<i>Schizachyrium scoparium</i>	3.58 \pm 0.39
<i>Euphorbia corollata</i>	3.57 \pm 0.37
<i>Sporobolus heterolepis</i>	2.96 \pm 0.39

Table 1. Continued.

Group 1: Dry sand sites. N = 9	
Species	Abundance
<i>Rosa caroliniana</i>	2.37 \pm 0.26
<i>Fragaria virginiana</i>	2.23 \pm 0.30
<i>Phlox pilosa</i>	2.23 \pm 0.29
Group 6: Wet prairies and wet dolomite prairies N = 9	
<i>Carex sp.</i>	6.27 \pm 1.81
<i>Solidago gigantea</i>	4.29 \pm 0.93
<i>Pycnanthemum virginianum</i>	3.69 \pm 0.85
<i>Calamagrostis canadensis</i>	3.48 \pm 1.46
<i>Spartina pectinata</i>	3.18 \pm 0.82
<i>Carex stricta</i>	2.78 \pm 2.10
<i>Fragaria virginiana</i>	2.73 \pm 0.83
<i>Helianthus grosseserratus</i>	2.67 \pm 1.14
<i>Solidago riddellii</i>	2.67 \pm 0.94
<i>Andropogon gerardii</i>	2.54 \pm 0.69

(flowering spurge), and *Stipa spartea* Trin. (porcupine grass), and the second group (hill prairies and dry dolomite prairies) also had high abundance of *Poa compressa* L. (Canadian bluegrass), *Euphorbia corollata*, and *Stipa spartea*. The two transitional groups are generally similar in species present.

Mesic sites were dominated by *Andropogon gerardii* but also had high abundance of *Sorghastrum nutans*, *Aster ericoides* L. (heath aster), and *Schizachyrium scoparium*. The group of mesic sites had some species in common with both the transitional sites as well as with hill prairies. The wet sites were fairly distinctive in their species composition. In addition to high abundance of *Carex* spp., they had high abundance of *Solidago gigantea* Ait. (late goldenrod), *Pycnanthemum virginianum* (L.) Dur. and Jacks. (mountain mint), *Calamagrostis canadensis*, and *Spartina pectinata*.

The geographic distribution of the sites (Fig. 2) shows that mesic sites were the most widespread, being found throughout the state. Hill prairies were most abundant along the bluffs of the Mississippi and Illinois rivers in the western part of the state, but were found in other locations. Dry sand sites, both transitional groups, and wet sites were more restricted in their distribution. Dry sand sites were located in west and west-central Illinois. Sites in the first transitional group were found mostly in western Illinois. The second transitional group was most abundant in north-central Illinois, particularly in Winnebago and Ogle counties. Finally, wet-mesic to wet sites were restricted to northeastern Illinois. This fit with the general pattern described in Corbett (1999), of a general trend of increasing dryness from northeast to southwest Illinois prairies.

The relationship between substrate and ordination group showed that "blacksoil" substrate generally corresponded well to the location of mesic prairies, as did loess hill and glacial drift. But in other cases, substrate did not correspond well with "ordination group"; sand and gravel were more widespread types, including mesic as well as dryer sites (Fig. 3). Correspondence between ordination group and soil association was generally not clear-cut (Fig. 4).

DISCUSSION

Generally, we saw a pattern of some species being widespread (for example, *Schizachyrium scoparium*) across several of the site-type groups, with the less-abundant or "subdominant" species being the ones that gave each group its distinctive character. There was also

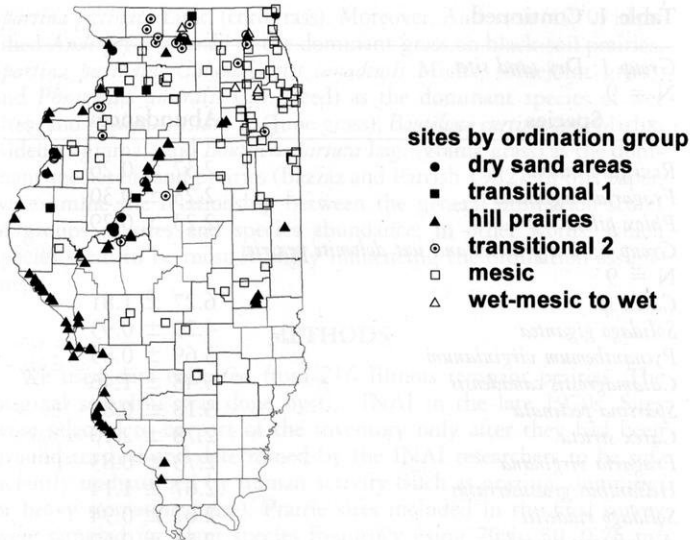


Fig. 2. Geographic pattern of ordination groups. Ordination group by geographic location. Ordination group was determined based on the results of a detrended correspondence analysis. Geographic locations of sites were from the IGIS CD-ROM set (IDENR 1996).

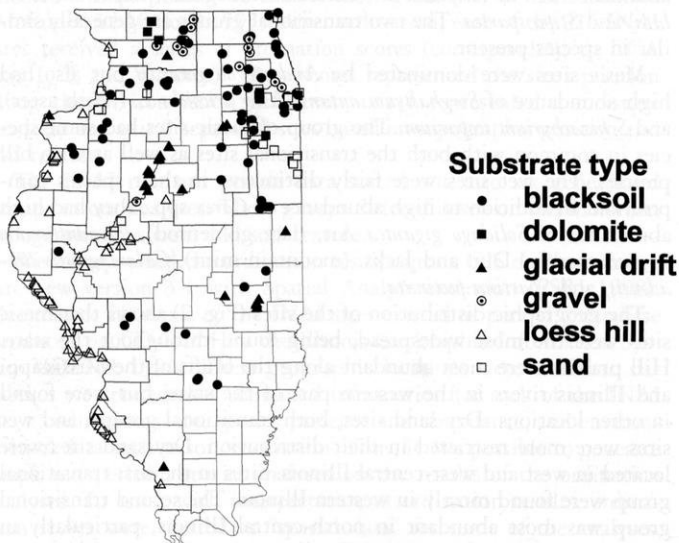


Fig. 3. Relationship between substrate type and geography. Substrate type by geographic location. Substrate type was based on determinations made by the original INAI survey of sites. Geographic locations of sites were from the IGIS CD-ROM set (IDENR 1996).

more overlap between the groups than we originally anticipated. Many species were shared, particularly between the hill prairies, transitional groups 1 and 2, and the mesic sites. The most distinctive species compositions belonged to either the extremely dry sand sites or the wettest sites. There was also some geographic separation of ordination groups, particularly the driest and wettest sites. These patterns generally agreed with those observed for other studies examining Illinois prairie (Nelson and Anderson 1983, Anderson 1991).

The dry sand sites were located on deep Pleistocene sand deposits. They had high abundance of *Schizachyrium scoparium*, as well as spe-

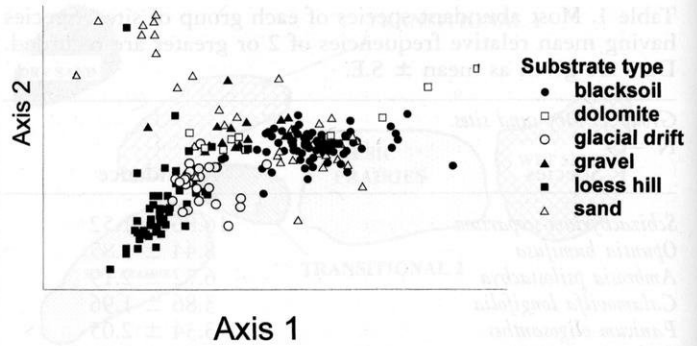


Fig. 4. Relationship between substrate type and ordination score. Ordination scores for sites were generated using Detrended Correspondence Analysis in PC-Ord. Ordination scores and substrate data were entered into ArcView version 3.1.

cies not found in other types of sites (*Opuntia humifusa*, *Ambrosia psilostachya*, and *Calamovilfa longifolia*). Many of these species were more characteristic of prairies further to the west, for example, the Nebraska Sandhills (Gleason 1922). These sites were almost entirely located in west or west-central Illinois, and there was a large cluster of them in Mason County along the Illinois River. These sites had distinctive environmental conditions, appearance, and species composition. (Hart and Gleason 1907, Gleason 1922).

Similarly, the wet and wet-mesic sites had a distinctive species composition. These sites were restricted to northeastern Illinois. A number of the wet sites had a dolomite substrate. These sites had high abundance of *Carex* spp., *Solidago gigantea*, *Pycnanthemum virginianum*, *Calamagrostis canadensis*, and *Spartina pectinata*. None of these species were found in high abundance in any of the other ordination groups. Nelson and Anderson (1983) determined that *Calamagrostis canadensis* was a dominant grass of wetter sites.

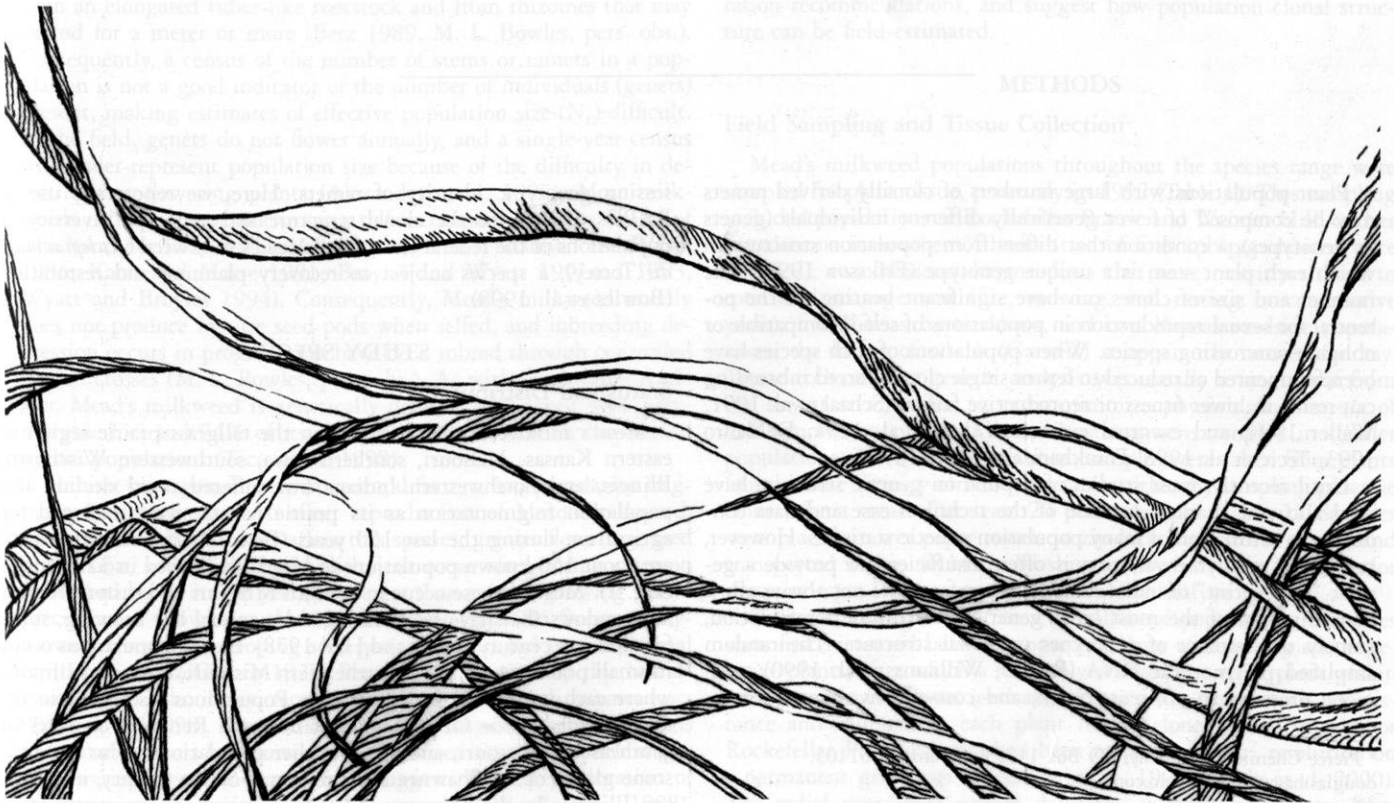
For the transitional sites and mesic prairies, there was more intergradation. All three groups had high abundance of *Euphorbia corollata*. In the transitional sites, *Schizachyrium scoparium* was the dominant species. It was present in mesic sites but at lower levels. *Schizachyrium* is generally considered to be adapted to dryer sites (Dhillon and Anderson 1994). *Andropogon gerardii* was the dominant in mesic sites. There was also some overlap between the transitional groups, mesic sites, and hill prairies. Hill prairies had *Schizachyrium scoparium* as the dominant species, but also had high abundance of *Bouteloua curtipendula* (also found in the second transitional group), *Sorghastrum nutans* (also found in mesic sites), *Dalea purpurea* (also found in the first transitional group), and *Euphorbia corollata* (also found in both transitional groups and the mesic sites). Many of these species were listed as species typical of "high lime prairies" by Curtis and Greene (1949) or as being abundant in Illinois hill prairies (Robertson et al. 1997).

Generally, substrate type or soil association did not correspond neatly with the pattern of ordination results. There was overlap of substrates between different site types (for example, there were mesic sand prairies as well as xeric sand prairies). There was some relationship between certain soil associations (Stokey-Alford-Muren, Seaton-Fayette-Stronghurst, and Clary-Clinton-Keomah) and hill prairies, but in other cases there was little relationship between site type and soil association. It seemed that the geographic pattern of site types within the state seemed to be more related to topographic position than to substrate—hill prairies on bluffs in southwest Illinois, and wet sites in low lying areas in the northeastern part of the state. "Distinctive" site types, such as dry sand prairies, tended to be located in geographically distinct areas, whereas mesic sites (and

both groups of transitional sites) tended to be more widespread. This suggested that certain species (*Andropogon gerardii*, *Euphorbia corollata*, and *Dalea purpurea*, for example) were widespread in Illinois and that other species (*Calamagrostis canadensis* and *Bouteloua curtipendula*, for example) were more restricted to specialized site types and may additionally be geographically restricted within the state. This has implications for prairie restoration; it is important to know both what species were historically present in the area as well as moisture availability and topographic characteristics of the site.

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Clonal Population Structure of the Federal Threatened Mead's Milkweed, as Determined by RAPD Analysis, and Its Conservation Implications

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Mead's milkweed (*Asclepias meadii* Torrey) is a formerly widespread outcrossing perennial prairie plant that has been listed as federal threatened. Clonal structure is one of several aspects of genetic variation relevant to strategies for restoration and conservation of this species. In the eastern part of its range, populations are very small and rarely, if ever, produce seeds, presumably because they comprise single or few clones. Only two large, sexually reproducing populations are known to exist, both in sites managed by prescribed burning. Most extant populations occupy Kansas and Missouri haymeadows, which are summer mowed, a process that prevents sexual reproduction by removing developing seed pods (follicles). These populations have apparently survived because of clonal spread. The random amplified polymorphic DNA (RAPD) technique was used to determine the clonal structure of 12 Mead's milkweed populations under different management regimes. RAPD analysis allowed determination of 1) the spatial pattern and clonal structure of populations and 2) how management histories (mowing vs burning) have impacted clonal structure. Burned sites had comparatively large numbers of genotypes with relatively small clones, while haymeadows had fewer genotypes and larger clones with significantly higher proportions of ramets per genotype. Because of Mead's milkweed's outcrossing breeding system, small fragmented populations are vulnerable to extinction if they comprise single clones, as evidenced by RAPD analysis. Populations in haymeadows are also not able to reproduce due to loss of seed pods and may have low reproductive potential if mowing has caused loss of genotypes. Restoration of new populations and conservation and management of small clonal populations will require infusion of multiple genotypes to facilitate successful outcrossing and seed production. Experiments will be required to determine the effects of novel genetic combinations on viability of restored milkweed populations.

INDEX DESCRIPTORS: *Asclepias meadii*, genotypes, haymowing, prairie management, viability.

Plant populations with large numbers of clonally derived ramets may be composed of fewer genetically different individuals (genets or genotypes), a condition that differs from population structure in which each plant stem is a unique genotype (Eriksson 1993). The number and size of clones can have significant bearing on the potential for sexual reproduction in populations of self-incompatible or obligate outcrossing species. When populations of such species have been fragmented or reduced to few or single clones, forced inbreeding can result in lower fitness or reproductive failure (Schaal et al. 1991, Weller 1994) and eventual extinction (Les et al. 1991, DeMauro 1993, Tecic et al. 1998, Frankham and Ralls 1998).

Until recently, most studies of population genetic structure have used allozyme markers because of the technical ease and data conducive to estimation of many population genetic statistics. However, multilocus allozyme variation is often insufficient to provide a genetic "fingerprint" of individuals and therefore does not always allow determination of the most basic genetic structure of a population, namely the number of genotypes or clonal structure. The random amplified polymorphic DNA (RAPD; Williams et al. 1990) technique provides an efficient, quick, and cost-effective means for as-

sessing genotypic identity of ramets. Here, we report the use of RAPDs to describe the clonal structure and genotype diversity of populations of the federal threatened Mead's milkweed (*Asclepias meadii* Torrey), a species subject to recovery planning and restoration (Bowles et al. 1998).

STUDY SPECIES

Status and Distribution

Mead's milkweed once occurred in the tallgrass prairie region of eastern Kansas, Missouri, southern Iowa, southwestern Wisconsin, Illinois, and northwestern Indiana but suffered rapid decline and population fragmentation as its prairie habitat was developed for agriculture during the last 150 years (Betz 1989). Presently, there are about 150 known populations of Mead's milkweed in 32 counties (Fig. 1). Most of these occur in western Missouri and eastern Kansas haymeadows that have been managed by annual hay mowing, some for almost a century (Fitch and Hall 1978). Eleven populations occur in small prairie remnants of northeastern Missouri, Iowa, and Illinois, where each has fewer than 25 plants. Populations also occur in igneous glades of the Ozark region of Iron and Reynolds counties in southeastern Missouri, and small outlier populations occur in sandstone glades of the Shawnee Hills region of Saline County, in southern Illinois. In the Shawnee Hills, fire protection apparently frag-

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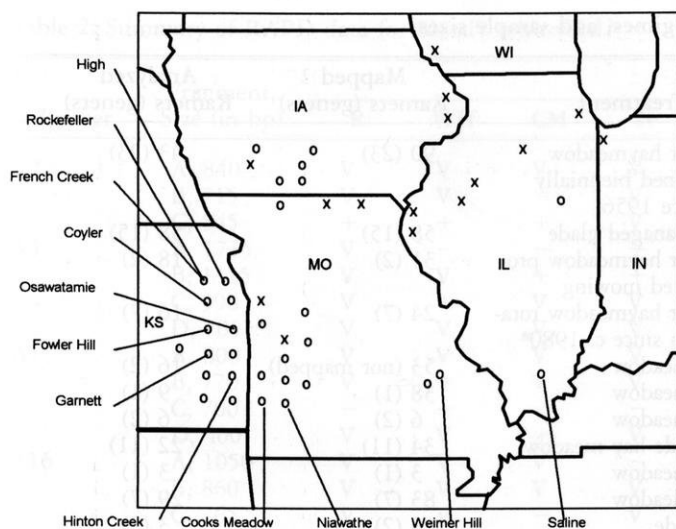


Fig 1. County occurrences of Mead's milkweed populations. Counties with extant populations are indicated by "o", counties from which populations have been extirpated are indicated by "x". Names correspond to Table 1.

mented a formerly widespread population into four small sub-populations in forest openings separated by distances of up to one kilometer. The largest of these sub-populations has about 20 stems, with far fewer plants in the other sites.

Biology and Ecological Interactions

Mead's milkweed is a long-lived perennial, producing ramets both from an elongated tuber-like rootstock and from rhizomes that may extend for a meter or more (Betz 1989, M. L. Bowles, pers. obs.). Consequently, a census of the number of stems or ramets in a population is not a good indicator of the number of individuals (genets) present, making estimates of effective population size (N_e) difficult. In the field, genets do not flower annually, and a single-year census will under-represent population size because of the difficulty in detecting non-flowering plants (Alexander et al. 1997). Most milkweeds exhibit late-acting ovarian self-incompatibility, the causes of which are not fully understood (Kephart 1981, Shannon and Wyatt 1986, Kahn and Morse 1991, Broyles and Wyatt 1991 and 1993, Wyatt and Broyles 1994). Consequently, Mead's milkweed usually does not produce mature seed pods when selfed, and inbreeding depression occurs in progeny that have been inbred through controlled garden crosses (M. L. Bowles, pers. obs.). As with many other *Asclepias*, Mead's milkweed is genetically diverse, with about 40% polymorphic loci and 74% of its allozyme genetic variation maintained within populations (Tecic et al. 1998).

Habitat management, environmental factors, and population fragmentation can interact to affect reproduction of Mead's milkweed. Fire and rainfall positively affect this species; greater flowering, seed production, and seedling establishment occur after dormant season prescribed burns and in years of greater than average growing season precipitation (Bowles et al. 1998, Kettle et al. 2000). Summer haymowing removes developing seed pods (follicles) and prevents sexual reproduction (McGregor 1977, Betz 1989). Apparently this has allowed very little, if any, recruitment of new genets in haymeadows (Tecic et al. 1998). Compared to those in haymeadows, milkweeds in burned habitats have lower ramet densities but greater percentages of flowering stems and are larger, suggesting greater allocation of resources into vegetative spread in haymeadows (Bowles et al. 1998).

Using allozymes, Tecic et al. (1998) found that fire-managed milkweed populations had greater numbers of multi-locus genotypes and lower ramet : genet ratios than haymeadows and postulated that haymeadow populations had lost genotypes due to attrition and lack of sexual reproduction. They also found that 64% of multi-locus genotypes occurred within single populations and that smaller population fragments tended to be comprised of single genotypes that presumably would be incapable of cross-pollinating and producing seeds. In fact, reproduction has seldom been observed in the smaller eastern populations of this species (Bowles et al. 1998, Tecic et al. 1998).

There are two known sexually reproducing populations of Mead's milkweed (Bowles et al. 1998, Tecic et al. 1998). About 200 or more plants occur on the 4.5-ha Rockefeller Prairie in Jefferson County, Kansas, where about 15% of flowering stems produce pods annually (Kettle et al. 2000). This former haymeadow is managed by the University of Kansas as an Ecological Reserve; since 1956 it has been fire-managed, with burns usually occurring in alternate years (Fitch and Kettle 1988, Kettle et al. 2000). One hundred or more plants occur in the largest igneous glade habitat, which occurs along about one kilometer of the exposed southwestern slope of Weimer Hill, in Iron County, Missouri (Fig. 1). This rugged habitat has escaped agriculture and haymowing but has undergone some forest encroachment resulting from reduced fire frequencies (Guyette and McGinnes 1982, Guyette and Cutter 1991, Ladd 1991). However, Weimer Hill is a state-owned and fire-managed natural area, where milkweeds produce seeds (M. Bowles and D. Hayworth, pers. obs.).

The aims of this study of Mead's milkweed populations were 1) to determine clonal structure by analyzing the spatial pattern of ramets and genets based on RAPD genotype fingerprinting and 2) to determine how different management histories (i.e., haymowing vs burning) affect clonal population structure. We compare these findings to those based on allozymes, make management and restoration recommendations, and suggest how population clonal structure can be field-estimated.

METHODS

Field Sampling and Tissue Collection

Mead's milkweed populations throughout the species range were sampled for plant tissue, primarily in 1992 (Table 1). This sampling included populations at Rockefeller Prairie and Weimer Hill, outlier populations in southern Illinois (two of four sub-populations were sampled), two Missouri haymeadows that were recently shifted to rotational management (fire, mowing, and resting in consecutive years), five Kansas haymeadows, and two Kansas roadside populations, the larger of which (Garnett) is apparently mowed for hay. Tissue collected for genetic analysis was usually a single leaf from the lowest stem nodes, so as to minimize physiological impact of leaf removal on plants. All visible stems were sampled in smaller populations. For larger populations, samples were taken from plants found in the vicinity of flowering ramets, thereby sampling putative clones, for a total of at least 20 plant samples (Table 1). Samples were placed on wet paper towels in zip-lock bags, stored on ice, and transported within 48 hrs to Washington University in St. Louis for tissue storage, DNA extraction and RAPD analysis.

To determine clonal patterns of milkweed populations, distances were first measured between apparent clones of flowering and vegetative plants, after which a randomly selected flowering plant within each putative clone was used as a center point from which the distance and azimuth to each plant in the clone was surveyed. For Rockefeller Prairie, plants had been mapped at 1-m² resolution on a permanent grid map (Alexander et al. 1997, Kettle et al. 2000). The radial coordinate system data (the azimuth, or degrees from

Table 1. Mead's milkweed population study sites, management regimes, and sample sizes.

Label	Population Site Name	County, State	Treatment	Mapped Ramets (genets)	Analyzed Ramets (genets)
R	Rockefeller	Jefferson, KS	former haymeadow burned biennially since 1956	90 (23)	43 (23)
WH	Weimer Hill	Iron, MO	fire-managed glade	58 (15)	58 (15)
CM	Cooks Meadow	Barton, MO	former haymeadow protected mowing	31 (2)	18 (2)
N	Niawathe	Dade, MO	former haymeadow rotation since c. 1980 ^a	24 (7)	16 (7)
C	Colyer	Douglas, KS	hay meadow	53 (not mapped)	16 (2)
FC	French Creek	Jefferson, KS	hay meadow	38 (1)	9 (1)
FH	Fowler Hill	Franklin, KS	hay meadow	6 (2)	6 (2)
G	Garnett	Anderson, KS	roadside hay meadow	34 (11)	22 (11)
H	High	Leavenworth, KS	hay meadow	3 (1)	3 (1)
HC	Hinton Creek	Bourbon, KS	hay meadow	83 (7)	29 (7)
O	Osawatomie	Miami, KS	roadside	3 (2)	3 (2)
S	Saline	Saline, IL	unburned glades	13 (2)	13 (2)
Totals					236 (75)

^a rotation between mowing/resting/burning years.

North, plus the meter distance from a point) and Rockefeller maps were converted to Cartesian coordinates, allowing stems and clones to be plotted for each population.

RAPD Methods

Upon receipt of field samples in the laboratory, they were promptly frozen in liquid nitrogen and stored in polypropylene tubes at -80°C . After grinding the frozen leaves with a prechilled mortar and pestle, genomic DNAs were obtained from approximately 5 mm^3 of the powder by standard CTAB extraction miniprep (Doyle and Doyle 1987). DNA concentrations were estimated using either a fluorometer or by comparison alongside standards in agarose gels; samples were then diluted to approximately $5\text{ }\mu\text{g}/\text{mL}$. Each $25\text{ }\mu\text{L}$ amplification reaction, performed in 0.5 ml tubes, contained 10 mM Tris-HCl pH 9.0, 50 mM KCl, 0.1% Triton X-100, 25 ng genomic DNA, 2.5 mM MgCl_2 , $50\text{ }\mu\text{M}$ each dNTP, 400 nM 10-mer oligonucleotide primer, and 0.625 U *Taq* DNA polymerase (Promega). After an initial 2 min denaturation at 95°C , polymerase chain reaction (PCR) cycling was for 40 repetitions of ramping between 1 min stops at 95°C , 37°C , and 72°C . The final cycle was amended for 10 min at 72°C before soaking at 4°C .

After an initial screen of about twenty arbitrary 10-mer oligonucleotide primers (Operon Technologies) for those which yielded repeatable variation among a small subset of the milkweed DNA samples, four were selected for use in assessing variation among all samples in the study. These were Operon Technologies primers A2, A3, A7, and A16. RAPD fragments produced by PCR were documented by UV-light photography of samples which had been electrophoresed in 2% agarose gels and stained with ethidium bromide. Contamination was monitored by including a negative control (i.e., reaction with all reagents except DNA) with each PCR. Each primer-DNA reaction combination was repeated at least once to ensure reproducibility of the resulting fragment profile, and assessment of fragment identities among individuals within a population was maximized by always running samples from the same population in the same gel. However, we do not assert with certainty the homology of like-sized bands among populations, especially because individuals

from different populations were not run alongside each other in the same gels.

A total of 236 samples from 12 populations were analyzed for RAPDs (Table 1). For the smallest populations, all collected and mapped samples were analyzed. For other populations, at least two samples were analyzed from each presumed clone. A greater number of samples was analyzed from Rockefeller and Weimer Hill populations. Among all 236 analyzed samples, 17 clear polymorphisms were scored for their presence or absence. Similarities (i.e., the number of shared band states per 17 total bands scored) were calculated for all pairwise combinations of individual RAPD profiles. This simple measure allowed detection of all pairs of individuals that differed by only 1 of 17 bands; these single character differences were rechecked to ensure that they were not the result of scoring errors. Such scrutiny of profiles differing by one character was crucial since the primary purpose was to determine genotypic identity from non-identity.

Data Analysis

The distribution of stems possessing each RAPD profile was indicated on coordinate maps of each population. This allowed visual comparison of the clonal structure suggested by the apparent grouping of stems in the field to that detected by RAPDs.

To test effect of burning versus hay mowing on the proportional abundance of ramets per genotype, we used a nested ANOVA on SYSTAT (1999), which uses least squares estimations to handle unbalanced designs. Because not all stems were assayed with RAPDs for each population, differences in absolute numbers of ramets per genet could not be tested. However, we assumed that sampling of ramets for RAPDs analysis within apparent clones was random, which provided stratified random sampling within populations. For analysis, the mean percentage of ramets per RAPDs genotype was calculated for each population. At the population level, this statistic represents the inverse of the number of genotypes multiplied by 100 and thus can be thought of as a measure of genotype diversity that is sensitive to sample size. Sites with one genotype (mean = 100%) were excluded from analysis as well as the Osawatomie roadside and

Table 2. Summary of RAPD data for Mead's milkweed.^a

Primer	Fragment, Size (in bp)	Population											
		R	WH	CM	N	C	FC	FH	G	H	HC	O	S
A2	A, 840	V	V	V	V	V	+	-	V	+	V	+	V
	B, 715	V	V	-	V	-	-	-	V	-	V	-	-
	C, 545	+	+	+	V	V	+	V	+	+	+	+	+
A3	A, 1735	V	-	-	-	-	-	V	-	-	-	-	-
	B, 1115	V	V	+	+	+	+	V	+	+	+	+	V
	C, 990	V	+	V	V	V	-	V	V	+	+	-	V
A7	D, 705	V	V	V	V	V	-	+	V	-	V	V	V
	A, 800	V	V	V	V	V	+	-	V	-	+	-	V
	B, 770	V	+	V	V	V	+	V	V	+	V	+	V
A16	C, 700	-	-	-	-	-	-	V	V	-	-	-	-
	D, 400	V	V	+	V	+	+	V	+	+	V	+	V
	A, 1050	V	V	V	-	V	+	-	+	-	V	-	V
	B, 860	V	V	V	V	V	-	V	V	-	V	V	-
	C, 765	V	V	-	V	V	-	-	V	-	V	V	-
	D, 710	V	-	V	-	-	-	V	V	-	V	-	-
Total variable bands	E, 655	V	V	V	V	V	-	V	V	+	+	+	V
	F, 1125	V	-	-	V	V	-	-	-	-	V	-	-
Total variable bands		15	10	9	12	11	0	10	11	0	10	3	9
Detected genets		23	15	2	7	2	1	2	11	1	7	2	2
Mean % ramets/genet		4.35	6.7	50	14.3	50	100	50	9.1	100	14.3	50	20

^a V = fragment variable in population; - = fragment absent from population; + = fragment fixed in population.

Saline County, Il., populations, which were neither burned nor mowed. Tested sites were nested within treatments as indicated in Table 1: burned (Rockefeller and Weimer Hill), former Missouri haymeadows that are now managed in rotation with fire, mowing and resting (Cooks Meadow and Niawathe Prairie), and Kansas Haymeadows (Coyler Prairie, Fowler Hill, Garnett, and Hinton Creek). To normalize heavily skewed data, the square root of each mean % was arcsine and log (Ln) transformed (Zar 1974). For comparison, we also calculated the putative number of ramets per genet among management treatments based on estimated clonal size (number of ramets per clone) using the mapped RAPD genotypes.

RESULTS

Genotypic Variation

A total of 17 polymorphic bands were scored among the 236 samples analyzed from 12 populations. Individual populations possessed from 7 to 16 of these amplified bands, and in no case was the presence or absence of a band unique to one population. The number of bands which were polymorphic *within* populations ranged from 0 to 15 (Table 2).

Among all samples, a total of 75 genotypes were specified by individual presence/absence profiles of the 17 RAPD bands. Only two such genotypes occurred among populations, in both cases at Garnett and Weimer Hill, leaving 97.3% restricted to single populations. The number of different RAPD profiles occurring in individual populations ranged from 1 to 23 (Table 2). Samples having identical RAPD profiles were nearly always spatially contiguous in the population, allowing them to be demarcated easily in clonal maps of each population (Fig. 2). This result is strong evidence that RAPD analysis successfully "fingerprinted" the samples, such that those plants having identical RAPD profiles can be interpreted as ramets of one genet. Within sites, the only exception occurred in Rockefeller, where two very widely spaced individual stems possessed iden-

tical profiles. These stems could have been derived from the same seed source or might be distinguished with additional primers.

Effects of Mowing and Burning on Clonal Structure

Burned sites had the greatest numbers of genotypes, with 23 genotypes identified at Rockefeller and 15 found among the Weimer Hill samples. In comparison to haymeadows, these genotypes appeared as relatively small clones, and only in a few instances were multiple genets (represented by a few stems) present within the same 1- or 2-m² area (Fig. 2). With one exception, 7 or fewer genotypes were found in each haymeadow. The Garnett roadside had 11 genotypes and a clonal pattern more similar to burned prairies than haymeadows. The only occurrences in haymeadows of multiple genets within small areas were once at Garnett and twice at Hinton Creek. Two native genotypes were identified among the two subpopulations that were sampled from Saline County, Il.

Clonal structure, as measured by the mean percent of ramets per genotype within populations, differed significantly between burned and unburned populations (Fig. 3). There were much lower ramet : genotype ratios (and more genotypes) in burned habitats than in unburned Kansas and Missouri sites (Table 2). Estimates of the total number of ramets/genet revealed the same pattern, with about 3 ramets/genet in burned sites and 8 to 9 ramets/genet in unburned sites. However, there was also high variation among individual sites (Table 2). For example, Hinton Creek and Garnett had lower ramet : genotype ratios than other Kansas haymeadows, and Niawathe Prairie had a much lower ramet : genotype ratio than Cooks Meadow.

DISCUSSION

Genotype Distribution and Its Reproductive Implications for Conservation

Analyses of population genetic structure in Mead's milkweed using allozymes and RAPDs revealed similar information, but with

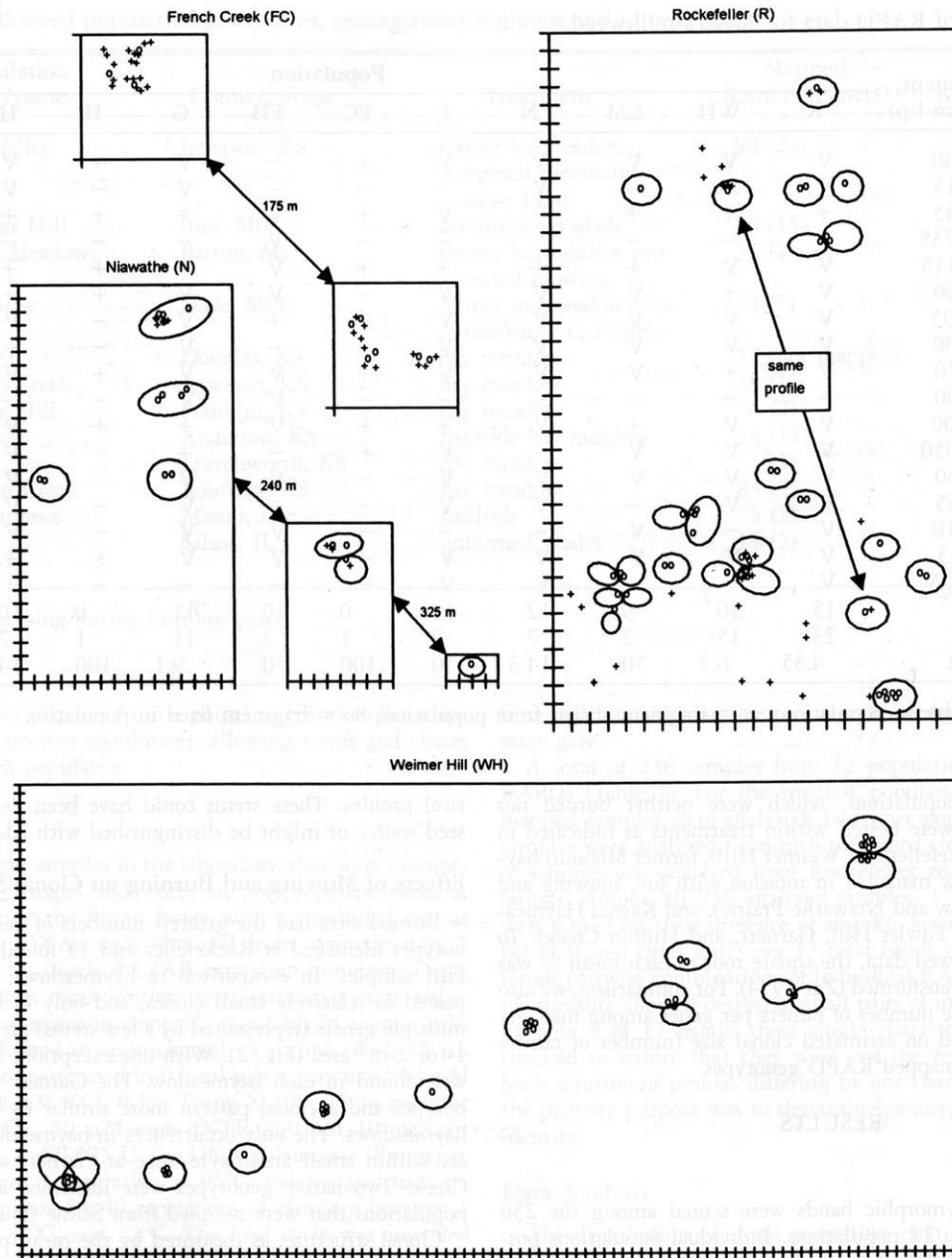


Fig. 2. Clonal structure of Mead's milkweed populations. Sampled and analyzed stems are indicated by "o", unanalyzed stems are indicated by "+". Open circles enclose genetically identical ramets representing single genets. Scale: axes hatch marks represent 5 m intervals, except for Weimer Hill, where hatch marks are at 10 m intervals. French Creek comprises one genet.

important differences. For conservation applications, population structure, as shown by hierarchical F-statistical analysis, can be supplemented by genotype information with important applications. For example, about 74% of the genetic diversity in Mead's milkweed, as measured by allozymes, is retained *within* populations (Tecic et al. 1998), as is characteristic for plants with outcrossing breeding systems and wind-dispersed seeds (Hamrick and Godt 1990). However, 97.3% of the RAPDs genotypes were restricted to single populations, and 64.2 % of allozyme multi-locus genotypes occurred in single populations (Tecic et al. 1998).

Although the genetic mechanism in late-acting ovarian self-in-

compatibility in milkweeds is poorly known, presence of high numbers of different genotypes, as measured by RAPD analysis, would appear to increase chances of reproduction. For example, 23 RAPD genotypes occurred among 43 samples at Rockefeller, and 15 RAPD genotypes occurred out of 58 samples at Weimer Hill, both sexually reproducing populations. Additional RAPDs genotypes at these sites might also have been identified with additional primers or with additional samples. Because clones are usually found only when they flower, and over 200 flowering stems have been estimated at Rockefeller (Alexander et al. 1997, Kettle et al. 2000), genets at these sites probably number in the hundreds. This suggests that a measure of

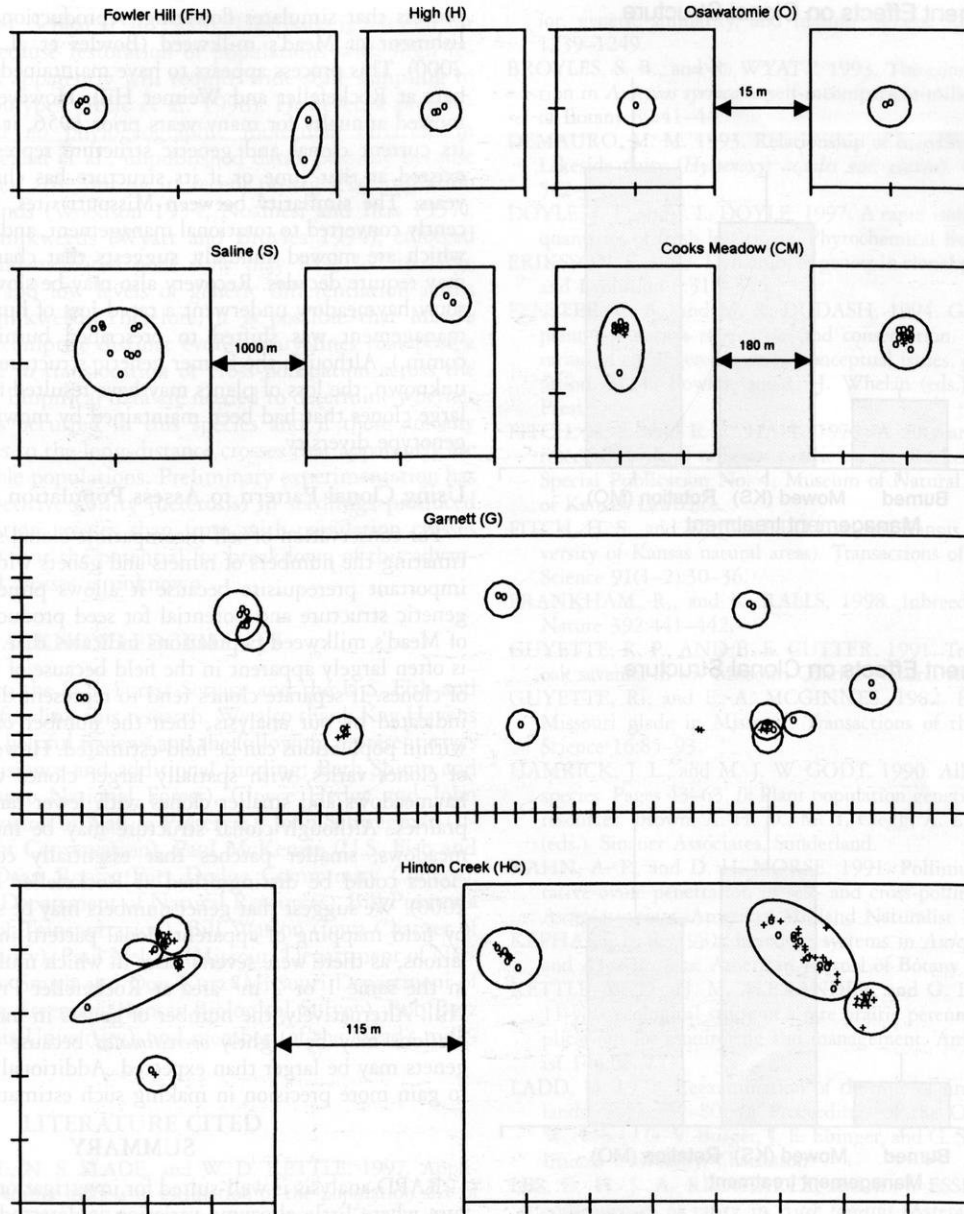


Fig 2. Continued

number of genotypes may be critical for assessing reproductive potential of natural populations and that maximizing genotype numbers may be an important strategy for restoring new milkweed populations. For restoration purposes, paradoxically, sampling among populations would be required to collect high numbers of genotypes despite retention of high genetic variation within populations.

Interactions Between Clonal Structure and Management History

The significant differences in clonal structure between fire-managed and mowed populations of Mead's milkweed have important biological and conservation implications. Although generally low levels of seed pod production occur in many milkweed species, including Mead's milkweed (Wyatt 1976, Betz 1989), differences be-

tween mowed and burned populations may represent a resource allocation trade-off between sexual and vegetative reproduction in this long-lived species (Bowles et al. 1998). If haymowing stops resource allocation toward sexual reproduction by removing maturing follicles, it may cause resources to be diverted toward increased clonal growth by spreading rhizomes. Conversely, sexual reproduction would reduce resource allocation that might go toward rhizomatous growth. Summer mowing probably also reduces competition from grasses and enhances further rhizomatous spread. Mowing may also stimulate lateral branching and increased growth of milkweed rhizomes in a manner analogous to pruning (Tecic et al. 1998). By these processes, mowing appears to stimulate clonal spread of Mead's milkweed.

The conservation implications of increased clonal growth in haymeadows appear critical, especially if accompanied by long-term at-

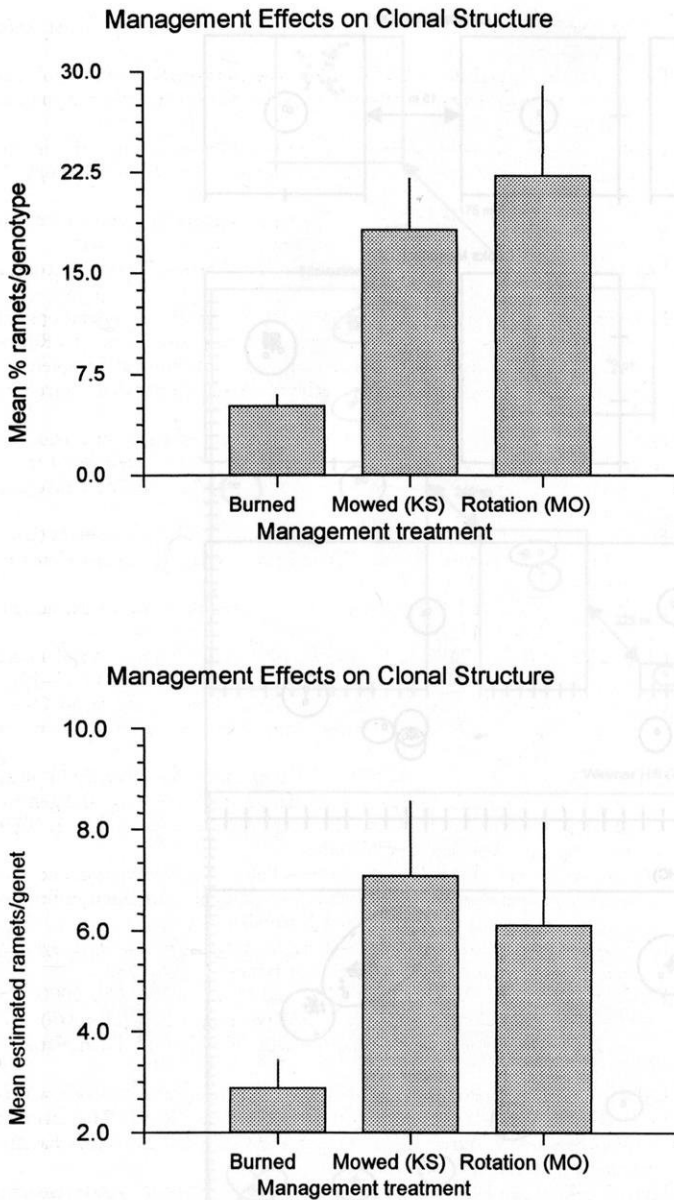


Fig 3. Effects of management on clonal structure of Mead's milkweed. Upper: mean % ramets/genotype (Nested ANOVA: Management $F = 7.16$, $P < 0.05$, Sites $F = 6.435$, $P < 0.001$). Lower: mean estimated ramets/genet. Burned = prescribed burned ($n = 2$), Mowed (KS) = mowed Kansas haymeadows ($n = 4$), Rotation (MO) = mowed, burned, rested Missouri haymeadows ($n = 2$).

trition of genotypes, which appears to be the case. This could result in either lack of reproduction (if prevented by self-incompatibility) or severe inbreeding depression from crosses within clones. Continued mowing could eventually result in populations that comprise few or single clones which could not sexually reproduce and might be highly vulnerable to other extinction processes, such as clonal disease. The extent to which mowing has had this effect is not fully known; however, the present data suggest that mowing should be avoided as a long-term management practice for Mead's milkweed populations.

As an alternative to mowing, fire-management represents a natural

process that simulates flowering, reproduction, and seedling establishment of Mead's milkweed (Bowles et al. 1998, Kettle et al. 2000). This process appears to have maintained high genotype numbers at Rockefeller and Weimer Hill. However, as Rockefeller was mowed annually for many years prior 1956, it is unknown whether its current clonal and genetic structure represents conditions that existed at that time or if its structure has changed in the last 45 years. The similarity between Missouri sites, which have been recently converted to rotational management, and Kansas haymeadows, which are mowed annually, suggests that change in these systems may require decades. Recovery also may be slow. However, one Missouri haymeadow underwent a rapid loss of hundreds of plants after management was shifted to prescribed burning (T. Smith, pers. comm.). Although the former genetic structure of this population is unknown, the loss of plants may have resulted from collapse of a few large clones that had been maintained by mowing with little loss of genotype diversity.

Using Clonal Pattern to Assess Population structure

For conservation of self-incompatible clonal species, accurately estimating the numbers of ramets and genets within populations is an important prerequisite because it allows projections of population genetic structure and potential for seed production. RAPD analysis of Mead's milkweed populations indicates that their clonal structure is often largely apparent in the field because of the spatial separation of clones. If separate clones tend to represent different genotypes, as indicated by our analysis, then the number of different genotypes within populations can be field-estimated. However, the relative scale of clones varies, with spatially larger clones with more ramets in haymeadows and smaller clones with fewer ramets in fire-managed prairies. Although clonal structure may be most apparent in haymeadows, smaller patches that essentially correspond to RAPD clones could be distinguished at Rockefeller Prairie (Kettle et al. 2000). We suggest that genet numbers may be slightly *underestimated* by field mapping of apparent clonal pattern in fire-managed populations, as there were several cases in which multiple genets occurred in the same 1 or 2 m² area at Rockefeller Prairie and at Weimer Hill. Alternatively, the number of genets in most hay meadow populations may be slightly *overestimated* because the spatial extent of genets may be larger than expected. Additional work will be needed to gain more precision in making such estimates.

SUMMARY

RAPD analysis is well-suited for investigation of population structure where little allozyme variation is detected (e.g., Brauner et al. 1992, Peakall et al. 1995, Reiseberg and Gerber 1995) and is ideally suited for examination of clonal genetic structure because only a high resolution discrimination of genotypes is necessary. For Mead's milkweed, a genetically diverse species, RAPD analysis of genotypes enhanced ramet mapping by identifying different patterns of clonal structure between mowed and burned populations. For this species, high numbers of genotypes appear to characterize sexual reproducing populations, and an important restoration objective should be to maximize numbers of genotypes within populations. Consequently, accurate estimates of the number of genotypes and their clonal structures are needed to assess the reproductive potential of populations and to help guide restorations. Our results indicate that field estimates of clonal structure based on occurrence of stems in "colonies" are accurate.

In addition to clonal and population genetic structure, phylogeographic analysis (Avisé et al. 1987, Avisé 1994) of the extent and relationship of separate evolutionary lineages within species may be helpful in guiding plant recovery and reintroduction strategies (Fens-

ter and Dudash 1994, Schaal et al. 1998). This issue is relevant for Mead's milkweed because restoration of populations with high reproductive potential apparently will require wide-scale sampling to obtain multiple genotypes (Tecic et al. 1998). However, a preliminary analysis found no phylogeographic molecular variation in Mead's milkweed (Schaal et al., unpublished data), possibly because such structure did not arise during its recent post-glacial migration from Ozarkian uplands (Woodson 1954, Noamesi and Iltis 1957). As in most other milkweeds (Wyatt and Broyles 1994), enforced outcrossing and wind-mediated gene flow may have led to large neighborhood sizes and low levels of genetic differentiation across the range of this milkweed. Therefore, it is possible that Mead's milkweed does not comprise distinct evolutionary lines that pose a concern with regard to translocation or cross-pollination across the range of the species. Empirical data are needed to determine whether local adaptation has occurred in this species and if there are any genetic consequences to the long-distance crosses that apparently are needed to build viable populations. Preliminary experimentation has found greater competitive ability (heterosis) in seedlings produced from among-population crosses than from within-population crosses (Bowles et al. 1998), but the potential for breakdown of this advantage with continued crosses is unknown.

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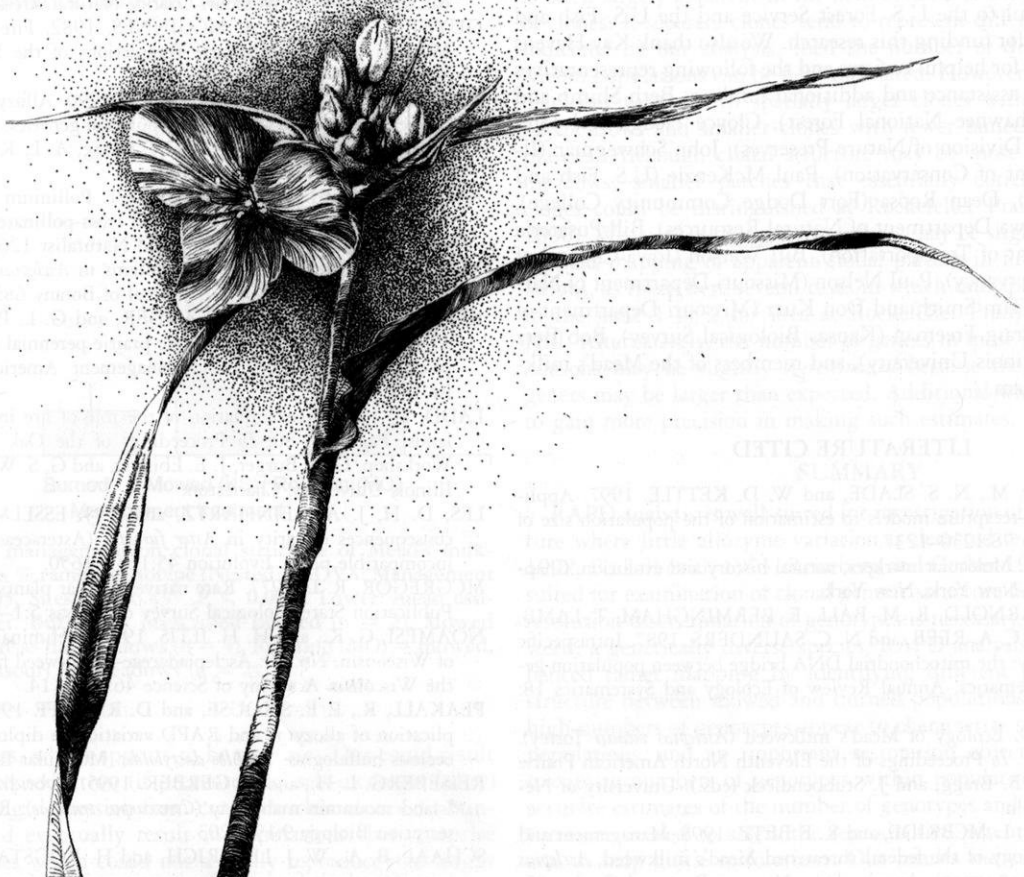
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Distribution Patterns of the Regal Fritillary Butterfly (*Speyeria idalia* Drury) within a Wisconsin Dry Prairie Remnant

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The Regal fritillary butterfly (*Speyeria idalia* Drury) is a grassland dependent species that may be fire sensitive in its egg, larval, and pupal stages. Considering distribution patterns when developing management strategies for *S. idalia* sites would increase individual survival. Our study objective was to determine the relationships between adult *S. idalia* distribution and habitat factors. We hypothesized that *S. idalia* prefers prairie patches with few shrubs, dominant native grasses, and violets, and that adult populations maintain a clustered distribution pattern within sites.

A 40 m × 40 m grid system was established in 1999 at a 32-hectare southwestern Wisconsin Nature Conservancy prairie preserve. Shrub cover, violet presence and abundance, and dominant grass type (native/non-native) were sampled for each grid cell. Transects bisecting grid cells were walked weekly during July and August, 1999, and *S. idalia* adults were counted for each grid cell. *S. idalia* were observed throughout the site, but were more frequent and more abundant in areas with favorable habitat characteristics. Areas with less than 10% shrub cover were utilized significantly more frequently than areas with more than 10% shrub cover ($\chi^2 = 7.134$, $df = 2$, $P = 0.028$), as were areas with violets ($\chi^2 = 11.156$, $df = 2$, $P = 0.004$) and native grasses ($\chi^2 = 9.980$, $df = 4$, $P = 0.041$).

INDEX DESCRIPTORS: *Speyeria idalia*, Regal fritillary, distribution, habitat, prairie, butterfly.

At a collection of prairie remnants in southwestern Wisconsin, the state endangered Regal fritillary butterfly, *Speyeria idalia* Drury, is a species of particular concern. The range of this species has been dramatically reduced over the past decade (Hammond and McCorkle 1983, Swengel 1993, Debinski and Kelly 1998), as has the number and size of remaining populations. This species was listed as state endangered in Wisconsin in January, 1998 (Wisconsin Natural Heritage Working List 1998).

Managers of sites where *S. idalia* is present lack data to better understand how to plan and implement natural community management such as brush cutting and prescribed fire. Distribution data would assist their efforts to promote habitat for this species and to minimize the potential for negative impacts on its population size and viability. Prescribed burning, for example, usually occurs during times of the year when this species is in its egg, larval, or pupal state and living low in the vegetation. Burning, therefore, may result in mortality of eggs, larvae, and pupae present above ground.

The distribution of *S. idalia* within remnant prairie sites places constraints on management applications. For example, if individuals of this species consistently concentrate in specific site areas, populations may become vulnerable to management that is applied at a large scale, such as fire. Under this scenario, it may be necessary to divide these areas into separate units and manage them in rotation so as to limit harm from any given management activity. In addition, recognizing the necessary habitat components for this species will assist habitat management planning. For example, if it could be determined that a threshold level of shrub cover existed above which habitat became inappropriate for *S. idalia*, managers could focus their management efforts to reduce shrub cover below this threshold level.

This study identifies vegetative factors affecting distribution of *S.*

idalia at a remnant prairie site in southwestern Wisconsin. Our question is, do certain vegetative and topographic factors influence or determine the distribution and/or abundance of *S. idalia* at the study sites? Researcher observations and preliminary analyses of the first year of fieldwork indicate that *S. idalia* utilizes certain areas of the study site preferentially over other areas and that four vegetative factors (shrub cover, native grass dominance, violet presence, and violet abundance) are associated with adult *S. idalia* distribution.

METHODS

Study Site

We studied *S. idalia* at a 32-hectare site comprised of high quality to highly degraded prairie remnants and pasturelands during the summer of 1999. Located near the border of Dane and Iowa counties in southwestern Wisconsin (T6N R5E Sec 17) (Fig. 1), the site was situated within mixed-use agricultural lands (actively cultivated fields, Conservation Reserve Program land, pastures, and woodlots) (Fig. 2). Although previously grazed, the study area had not been managed with prescribed burns.

A grid system composed of 109, 40 m × 40 m grid cells was installed at the site using a hand-held compass and metric fiberglass field tape in May and June 1999 (Fig. 3). A grid system was utilized so as to be able to correlate measured topographic and vegetative variables with butterfly observations across each site. Grid intersection points were marked with flags that were each labeled with a letter-number code denoting grid location. Grid cell size was based on the recommended maximum sight distance of 20 m for monitoring *S. idalia* along transects (West 1998). In our design, half of each grid cell was surveyed on either side of the transect bisecting



Fig. 1. The study site (starred) is located in east-central Iowa County in southwestern Wisconsin.



Fig. 2. Barneveld Prairie is situated amongst mixed-use agricultural land (actively cultivated fields, CRP land, pastures, and woodlots). The southern edge of the town of Barneveld is in the upper right of the aerial photograph.

the cell. Estimates of shrub cover, dominant grass type (native/non-native), and the presence/absence and abundance of violets, the larval host plant of *S. idalia* (Scott 1986), were made for each grid cell.

Shrub Cover

Shrub cover was estimated using a line-intercept technique along parallel transect lines (Elzinga et al. 1998). Distance of intercept (in five-cm increments), was recorded for shrubs and trees encountered along the transect for each grid cell. Shrub intercepts spaced 25 cm or less apart were treated as one continuous intercept.

Ocular estimates of shrub cover were also made for each grid cell by range class (0–10%, 10–20%, 20–50%, and 50–100% shrub cover); cover estimates were made from within each grid cell, and the approximate percentage of grid cell area covered by shrubs, as if seen from above, was estimated.

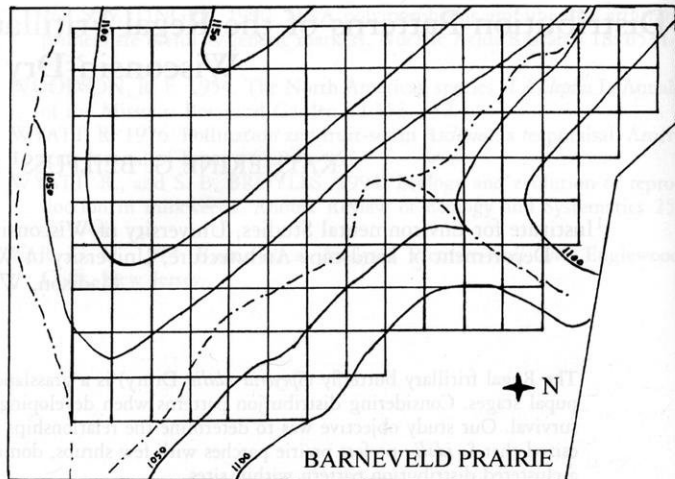


Fig. 3. A 40 m × 40 m grid system was installed at Barneveld Prairie with grid lines oriented in a N/S direction. A grid system was utilized to correlate topographic and vegetative variables measured with butterfly observations across each site.

Dominant Grass Type

The dominant grass type was recorded for each grid cell using three broad categories: exotic grasses dominant, exotic and native grasses co-dominant, and native grasses dominant. If native grasses such as *Bouteloua curtipendula* and *Stipa spartea* were present in greater percent cover than exotic grasses such as *Bromus inermis*, the grid cell was assigned the dominant grass type “native.” If the grasses present were primarily exotic, the grid cell was assigned the dominant grass type “exotic.” If roughly half of a grid cell could be classified “native” and half could be classified “exotic,” the cell was assigned the dominant grass type “mixed.”

Violets

During May 2000, a meander survey was conducted through each grid cell to record the presence of violets. The survey involved walking back and forth across each grid cell at 10 m intervals so that all portions of the cell were surveyed. When the first violet was observed within a cell, the search was ended in that cell and the observer moved to the next cell. Different violet species were not distinguished in the survey as *S. idalia* larvae appear to utilize all violet species (Hammond and McCorkle 1983, Opler and Krizek 1984, Scott 1986, Nagel, et al. 1991, Kopper 1997). *Viola pedata* and *V. pedatifida* dominated at this site.

From the 55 cells in which violets were recorded as present, 22 were randomly selected to be sampled for violet abundance. For each of these grid cells, 16 stratified random 3.14 m² circular quadrats were sampled in each grid cell to record violet abundance. Each quadrat received a score of zero (no violets present), one (one to two violets present), or two (three or more violets present); the scores from each of the sixteen quadrats were summed for a total “violet score” for each cell.

Transect Surveys

Surveys of adult *S. idalia* were conducted from 6 July through 26 August 1999 along transects that bisected grid cells using methods modified from Brown and Boyce (1998) and West (1998). All *S. idalia* individuals observed within 20 m of either side of the transect were counted, and the grid cell location, behavior (flying, resting,

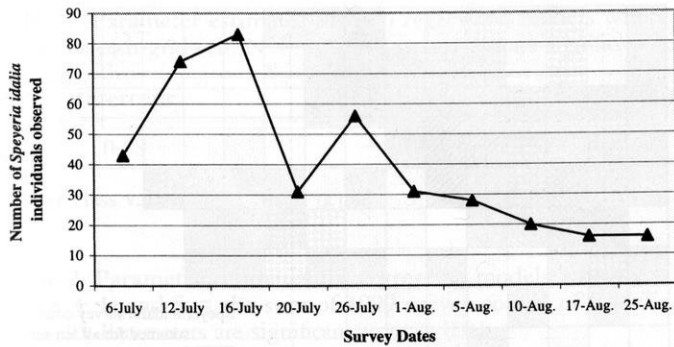


Fig. 4. Survey dates and number of *Speyeria idalia* individuals observed during each survey in 1999. Weather conditions were at the limit of prescription for the July 20 survey (cooler and cloudy, with rain following the survey), and this may account for the lower numbers observed during that survey.

nectaring, and mating), and (when possible) sex of each individual were recorded. In cases where the observed individual was flying, the grid cell over which it was flying when first observed was recorded. Plant species used for nectaring were noted for feeding individuals. Care was taken to avoid counting individuals more than once within a grid cell and between adjacent grid cells along a transect. Prevention of re-counting on different transects was impossible as individuals could not be tracked over time and distance. Because this study focused on distribution and not on estimating overall population numbers at the study site, we were not as concerned about double counting of individual butterflies between transect lines.

Eleven 160–600 m transects in a North/South direction were surveyed at Barneveld Prairie (Fig. 3). Surveys were conducted every

four to ten days. All transects were walked during each survey. Start and end times for each transect were recorded to estimate survey time per grid cell. Transects were divided into three groups and the survey order of these transect groups was randomized for each visit.

Surveys were conducted between 1000 and 1500 CST on clear or partly cloudy days when wind speeds were less than 24 kph and temperatures were 24°–34°C. Teams of two people conducted butterfly surveys, with the primary investigator or one other trained individual always doing butterfly observations and the second individual recording data.

Data Analyses

Data on sum of survey counts, shrub cover, dominant grass type, average survey time per grid cell, violet presence, and violet abundance were compiled for each grid cell. Using sum of survey counts as the dependent variable, multiple regression analyses were conducted with shrub cover, dominant grass type, violet presence and violet abundance as possible independent variables using several techniques of variable selection (e.g., backwards elimination and best subset selection) with the software package SAS (SAS Institute Inc. 1999). The data for sum of survey counts were skewed; residual plots were evaluated to assess if a transformation could minimize the problem. It was found that a log transformation of the independent variable ($\log[y+1]$) was most effective. Chi-square tests were also conducted to test the relationship between survey counts of *S. idalia* and measures of shrub cover, violets, and dominant grass type. Data on survey counts and on vegetation data were placed in categories (e.g., survey counts were allocated to 3 categories of 0, 1–5, and >5) for these analyses. Poisson goodness of fit testing was used to determine if *S. idalia* were distributed randomly, uniformly, or clustered.

Distribution of regal fritillaries at Barneveld Prairie (Iowa Co., WI) for each of ten surveys (July 6 - August 25, 1999)

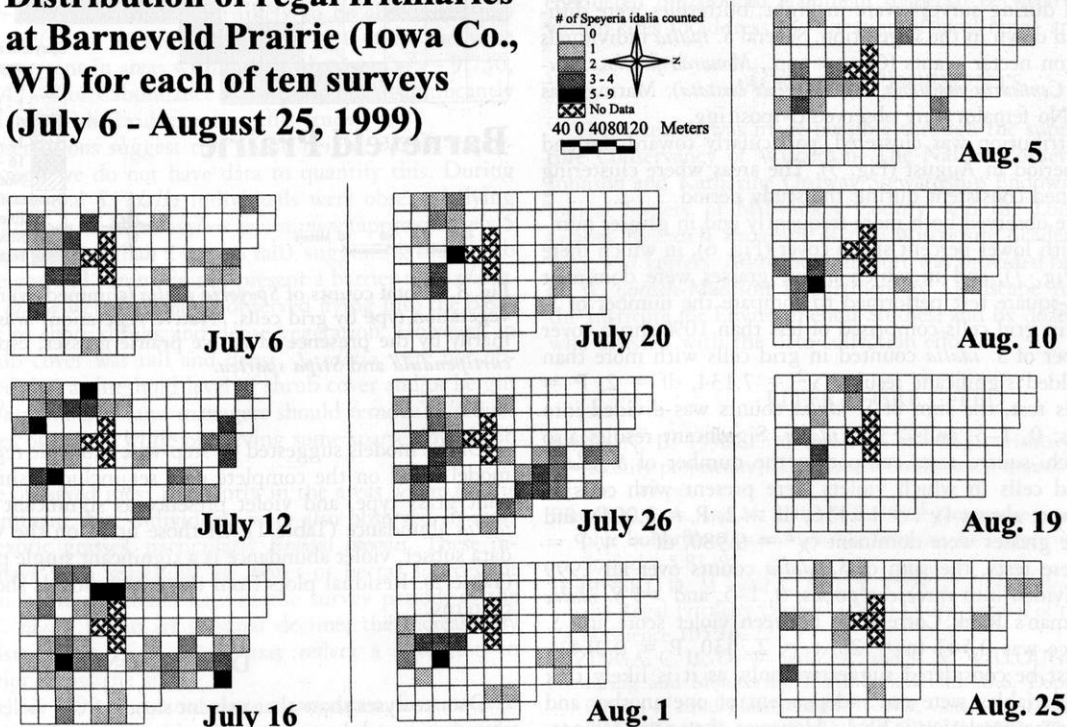


Fig. 5. Distribution of *Speyeria idalia* at Barneveld Prairie (Iowa Co., WI) for each of ten surveys conducted July 6–August 25, 1999.

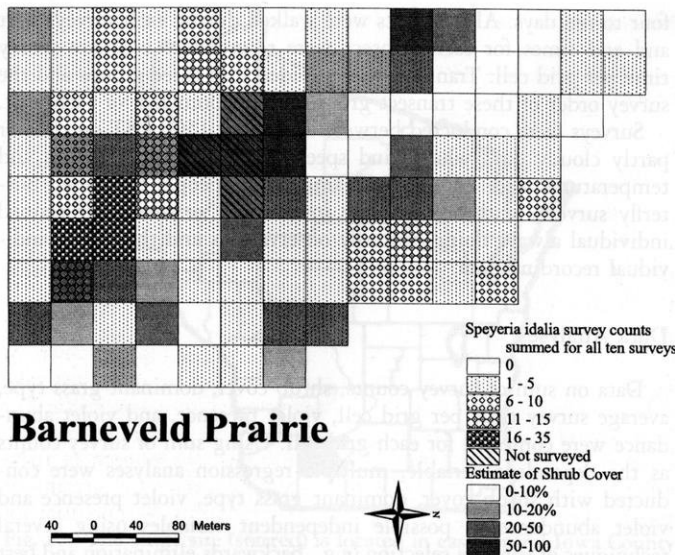


Fig. 6. Total counts of *Speyeria idalia* (summed over ten surveys) and shrub cover by grid cells. Shrub cover (by range class) is from ocular estimates.

RESULTS

Barneveld Prairie was surveyed 10 times between 6 July and 25 August, 1999; the average number of days between surveys was 5.56 days (Fig. 4). The peak of *S. idalia* numbers occurred in early- to mid-July and tapered through the end of the survey period (weather at the margin of survey parameters likely accounts for the dip in numbers for the 20 July survey). These observations were in keeping with those of other researchers of this species (Nagel et al. 1991, Barton 1996, Kopper 1997, West pers. comm.). The majority of *S. idalia* observed during surveys were in flight; butterflies were difficult to see when down in the vegetation. Several *S. idalia* individuals were observed on nectar plants (*Cirsium* spp., *Monarda fistulosa*, *Ratibida pinnata*, *Centaurea maculosa*, and *Verbena bastata*). Mating was also observed. No females were observed ovipositing.

S. idalia distribution was clustered, particularly toward the end of the survey period in August (Fig. 5). The areas where clustering occurred remained consistent during the study period.

S. idalia were observed both more frequently and in greater numbers in areas with lower percent shrub cover (Fig. 6), in which there were violets (Fig. 7), and in which native grasses were dominant (Fig. 8). A chi-square test performed to compare the number of *S. idalia* counted in grid cells comprised of less than 10% shrub cover with the number of *S. idalia* counted in grid cells with more than 10% cover yielded significant results ($\chi^2 = 7.134$, $df = 2$, $P = 0.028$). For this test, the sum of *S. idalia* counts was divided into three categories: 0, 1-3, and >3 *S. idalia*. Significant results also resulted from chi-square tests comparing the number of *S. idalia* counted in grid cells in which violets were present with cells in which violets were absent ($\chi^2 = 11.156$, $df = 2$, $P = 0.004$), and in which native grasses were dominant ($\chi^2 = 9.980$, $df = 4$, $P = 0.041$). For these tests, the sum of *S. idalia* counts over all 1999 surveys were divided into three categories: 0, 1-5, and >5 *S. idalia* counted. Spearman's Rank Correlation between violet score and *S. idalia* abundance was 0.543 ($n = 20$, $r = 2.7430$, $P = 0.0143$). These tests must be considered suggestive only, as it is likely that the vegetation variables were not independent of one another and because spatial autocorrelation is likely. However, they provided preliminary assessments of the importance of these variables.

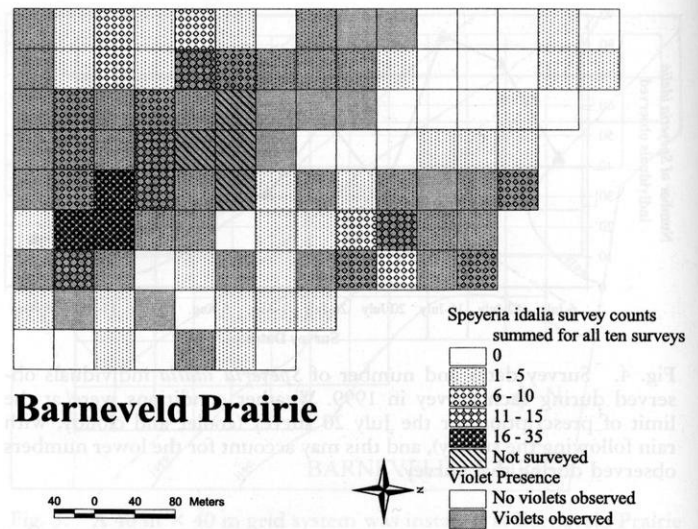


Fig. 7. Total counts of *Speyeria idalia* (summed over ten surveys) and violet presence by grid cells. Violet presence was determined by meander surveys in May, 2000.

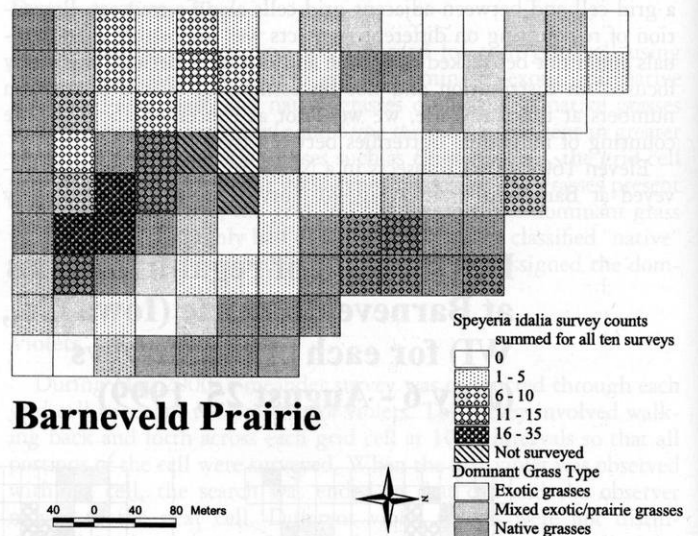


Fig. 8. Total counts of *Speyeria idalia* (summed over ten surveys) and vegetation type by grid cells. "Native vegetation" was determined primarily by the presence of native prairie grasses, especially *Bouteloua curtipendula* and *Stipa spartea*.

Of the models suggested by step-wise multiple regression, the best model fitted on the complete data set included shrub cover, dominant grass type, and violet presence as significant predictors of *S. idalia* abundance (Table 1). Of those fitted on the violet abundance data subset, violet abundance is a significant single predictor variable (Table 2). Residual plots from these two models showed no obvious patterns.

DISCUSSION

Data analyses show that percent shrub cover, violet presence, violet abundance, and dominant grass type are the most meaningful habitat factors for predicting *S. idalia* abundance in this study. The two best

Table 1. Parameter estimates for two regression models where $y = \log(s + 1)$ and $s =$ the sum of 1999 survey counts of *Speyeria idalia* for each grid cell. $N = 104$. All parameters are significant to $\alpha = 0.01$.

Intercept	Shrub Cover ^a	Dominant Grass Type	Violet Pres.	R ²
0.88	-2.17	0.05	0.54	0.273

^aCover class values (1-11) from ocular estimates.

Table 2. Parameter estimates for regression models where $y = \log(S + 1)$ and $S =$ the sum of 1999 survey counts of *S. idalia*. $N = 20$. Parameters are significant to $\alpha = 0.01$.

Intercept	Violet abundance	R ²
0.78	0.058	0.253

multiple regression models in which all variables were significant contained these four habitat factors (Tables 1, 2).

The clustered distribution of *S. idalia* observed in 1999 also supported this conclusion (Fig. 5). The areas of *S. idalia* concentration corresponded to the areas of highest quality prairie vegetation (i.e., dominance of native grasses), areas with less than 10% shrub cover and in which violets were present (Figs. 6, 7). However, it was unclear which factor or factors are ultimately causal in this relationship. It may be that nectar plant abundance was higher in these areas, and that this factor, not the "quality" of vegetation *per se*, was responsible for drawing *S. idalia* to these areas.

The fact that *S. idalia* abundance was positively correlated with the presence and abundance of violets may reflect the violets' presence in higher quality prairie vegetation and their absence in more disturbed areas dominated by exotic species (including areas with dense shrub cover). Violets were more likely to be absent in areas with exotic grasses ($\chi^2 = 10.886$, $df = 2$, $P = 0.004$), and were more likely to be present in areas with low shrub cover ($\chi^2 = 9.736$, $df = 4$, $P = 0.045$). Violet abundance was weakly but insignificantly negatively correlated with shrub cover in this study.

Researcher observations suggest that shrub height was an important factor, although we do not have data to quantify this. During surveys in 1999, several *S. idalia* individuals were observed flying over short, small clones of *Xanthoxylum americanum* (approximately 5 meters in diameter and less than 2 meters tall), suggesting that shrub clones of that height and extent do not present a barrier to *S. idalia*. Additionally, *S. idalia* were frequently observed flying into the bases of small clumps of short shrubs and dense vegetation. However, in areas where shrub cover was tall and dense, *S. idalia* were not observed. It may be that a threshold level of shrub cover and/or height exists for *S. idalia*, and that land managers should remove or reduce large, tall patches of shrubs while preserving some sparse, low shrub cover.

S. idalia were observed most frequently in the areas where prairie grasses were dominant, but individuals were also observed in areas dominated by exotic grasses, particularly *Bromus inermis*. These individuals may have been searching for mates or nectar sources, or moving between habitat patches. Late in the survey period, as the population of *S. idalia* began its seasonal decline, the increasingly concentrated distribution of *S. idalia* may reflect a reduction in searching behavior across the site.

Data collected in 1999 suggested three conclusions. First, that *S. idalia* appear to prefer areas with native prairie grasses over areas with primarily exotic grasses. Second, that *S. idalia* avoid areas with

high shrub cover but do utilize areas with low shrub cover. Finally, that *S. idalia* abundance is positively correlated with violet presence and abundance. These results suggest that land managers should continue efforts to maintain and restore remnant prairies where *S. idalia* occur, although the management techniques used must take into account the life history and distribution pattern of *S. idalia*. For sites where *S. idalia* are concentrated in specific areas, management units should be established so that only portions of each of these areas are managed by any one technique (e.g., mowing, grazing or prescribed fire) in a given year in order to minimize potential for mortality of *S. idalia* eggs, larvae, or pupae. Careful timing of management events may also reduce mortality. Finally, land managers should focus shrub-clearing efforts on dense shrub patches.

These conclusions are based on one season of survey effort. Monitoring of *S. idalia* populations, including their distribution across sites, must occur regularly in concert with management decisions, as populations of *S. idalia* are believed to fluctuate drastically from year to year (The Association for Biodiversity Information 2000). In addition, the distribution of this species across sites may vary from year to year. To begin to address the issue of annual variation, *S. idalia* surveys described in this paper will be repeated in 2000 to determine whether the distribution observed in 1999 is consistent from year to year. This work is also being carried out at a second, nearby site to determine whether the patterns observed at Barneveld Prairie hold true elsewhere. Finally, a mark-recapture study will be conducted in 2000 to document dispersal between and movement within sites to address the question of local range and distribution.

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The Decline of the Arogos Skipper (*Atrytone arogos*) at Prairie Coteau in Pipestone County, Minnesota

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In 1986, Prairie Coteau Scientific and Natural Area, Pipestone County, Minnesota was purchased by the Minnesota Department of Natural Resources and moved from management by grazing to a regime of fire management with some mechanical removal of weedy plants. Butterfly surveys were carried out on transects across the 133 ha. in 1988, 1989, and 1990 by Gerald Selby. The Arogos skipper *Atrytone arogos* was found and recorded along those transects. Follow-up surveys were completed in 1995, 1996 and 2000 by this investigator, at which time encounters with the species had dropped from a high of 48 on two days near the peak of the flight period in 1990 to zero in 1995, two in 1996 and two in 2000. There is, therefore, concern that *Arogos* populations will not be viable on this prairie through the next decade.

INDEX DESCRIPTORS: Arogos skipper, *Atrytone arogos*, Prairie Coteau SNA, prairie butterflies, prairie.

Our remaining prairie sites with their extensive invertebrate fauna have survived to our time by grazing/haying regimes. Changes in the management regime from virgin prairie to pasture or hay land surely caused changes in the invertebrate faunal composition. However, as of the middle of the 1900s, all of the known tallgrass prairie butterflies survived on many remnants. Associated with the time frame of the change from grazing/haying to fire-based management, several prairie butterflies have been extirpated from sites under private or governmental preservation and even from states, while other species are in decline (Schlicht and Orwig 1992).

While fire management is widely applied, few investigations have been done to determine the effects of management on true prairie obligate invertebrates before the management was applied, and fewer yet for a long time span. Some researchers have investigated insects, often mostly generalist prairie species on portions of relic sites, but studies were conducted after fire had already been applied in previous years. Therefore, they investigated an already fire influenced or modified fauna. This investigation does not accomplish the goal of pre-management monitoring, but it does provide population monitoring over a relatively long span of years for the Arogos skipper.

BACKGROUND

The Arogos skipper (*Atrytone arogos iowa*) is one of a contingent of prairie obligate butterflies of the tallgrass prairie biome. Prairie obligate butterflies are restricted to various native prairie plants for larval food and use plant structure or the ground thatch for diapause position and for hibernacula. These species are now restricted to isolated prairie remnants, and, therefore, with few exceptions, are not able to re-colonize if they are extirpated from a site.

The Arogos skipper was first described as *Hesperia iowa* by Scudder in 1868 using type specimens from Denison and New Jefferson, Iowa. The current designation is *Atrytone arogos* (Boisduval and LeConte) or *Atrytone arogos iowa* (Scudder) (Miller and Brown 1981). It is a small (2.7 cm) tan skipper with a dark border above and unmarked tan below. This species lives in part of a temporal sequentially on sites with other prairie obligate butterflies. It follows

the Poweshiek Skipperling (*Oarisma poweshiek*) in apparent phenological displacement (Schlicht and Orwig 1992). It is believed to use big bluestem (*Andropogon gerardi*) as a larval foodplant. The fourth stage larvae hibernate in silken tubes in the leaf litter (Opler and Krizek 1984), and they are therefore vulnerable to fire throughout their life cycle. The Arogos skipper is rare and in decline throughout its range, as are many other prairie butterflies (Glassberg 1999, Orwig and Schlicht 1999). Populations in Atlantic coastal states of a different subspecies are small, and some populations are apparently extirpated. Those states, New Jersey and Virginia for example, list the subspecies as threatened or endangered. It is a special concern species in Minnesota and Iowa.

METHODS

The first surveys at Prairie Coteau were done in 1988, 2 years after grazing ceased and fire management started on the south unit. Also, surveys were initiated for the remainder of the site the same year (G. Selby, pers. comm). During the summers of 1988 and 1989, Gerald Selby undertook an ambitious project to conduct "(1) general surveys for all butterfly species present at Prairie Coteau during each of the major flight periods, (2) to produce distribution maps for selected rare butterflies, and (3) population monitoring for *Hesperia dacotae* and other rare butterflies which were flying during its flight period" (G. Selby, 1989 unpublished). His 1990 project included ecological studies and response to management (Selby 1990). Both studies involved surveys for *A. arogos*.

Prairie Coteau Scientific and Natural Area (SNA) is a 133 ha dry hill prairie in Pipestone County, Minnesota (Township 108 North, Range 44 West, parts of Sections 29 and 32), that was first acquired, in part, in 1986. The soils are stony glacial till with some loess on the flatter high areas. Mesic to wet prairie elements, including butterflies, are found on lower areas. The site had a large hay field in the center, and most was grazed in the past (Fig. 1).

Selby placed transects every 100 m across the site and walked the transects every few days, identifying and counting each species that was within 5 m of the line or ahead of the single observer. Surveys

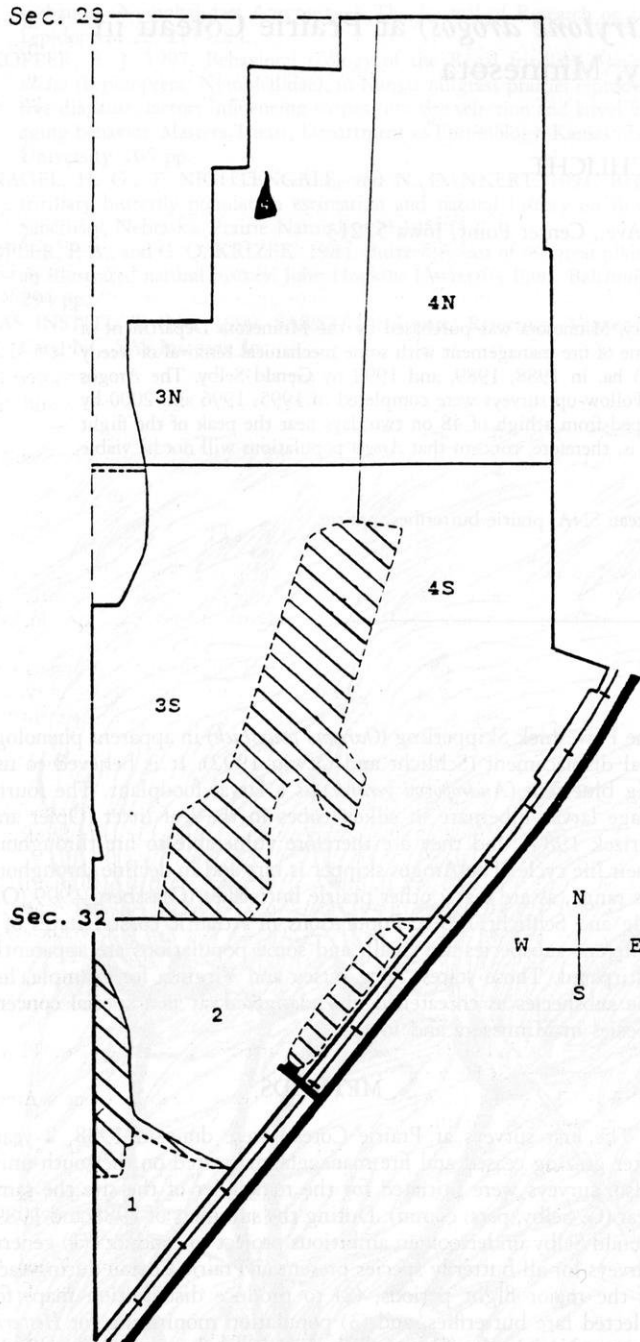


Fig. 1. Prairie Coteau SNA, Pipestone County, Minnesota (former cropland stippled, units are labeled) (from Selby 1990).

were conducted from 22 June to 13 July, 1988; 26 June to 17 July, 1989; and 23 May to 30 July, 1990 between 0900 and 1700 hours local time. Encounters were logged and recorded on maps.

In 1995, I began a two yr project which included Prairie Coteau SNA. In an effort to have data that could be compared to Selby's baseline work, I used his transects and protocol at Prairie Coteau SNA. The site was visited on 27 June 1995, 6 July 1995, 11 July 1995, 5 July 1996, 10 July 1996, and 15 July 1996 by one observer. Observations were done between 1000 and 1800 hours at tempera-

Table 1. Calendar day comparison for *Atrytone arogos* at Prairie Coteau SNA.

Year	Date/Dates	Number of <i>arogos</i>
1988	July 11 + 13*	9
1989	July 13 + 14*	46
1990	July 12 + 13*	48
1995	July 11	0
1996	July 15	2
2000	July 13	2

* Selby 2 day surveys to cover the site once.

Table 2. Comparison of data pair transect surveys for *Atrytone arogos* at Prairie Coteau SNA.

	1988	1989	1990	1995	1996	2000
6(27-28)	1			0		
6(29-30)		1				
7(1-2)		1	1			
7(3-4)		5	3			
7(5-6)	12	6	6	0	0	
7(7-8)	4	27				
7(9-10)		46			0	
7(11-12)	7	37	6	0		
7(13-14)		46	42			2
7(15-16)		40	39		2	
7(17-18)		2	10			
7(19-20)						
7(21-22)						
7(23-24)			21			
7(24-26)						
7(27-28)			16			

tures between 21° and 35° C, wind speeds below 23 kph, with cloud cover up to 90% if the temperature was above 26° C.

Another survey was made on 13 July 2000 with two observers following Selby's transects. The weather was within the described parameters, and recent management was recorded.

RESULTS

During the 1988 field season, Selby recorded 24 *Arogos* skippers on his transects. The first was seen on 22 June and his last on 11 July when he stopped surveying. In 1989, he surveyed later and saw a total of 211. The first individuals were seen on 5 July and the last on 17 July, his last survey day. During 1990, he counted and mapped 144 individuals, the first on 2 July and the last on 28 July.

The survey results in 1995-1996 were very different. In 1995, the first survey was on 27 June, probably too early for *Arogos* skippers, but the same day that Selby saw his first in 1988. However, none were seen. On 6 July and 11 July none were seen either, but the 11 July date should have been during the beginning of peak abundance. In 1996 no specimens were seen on 5 or 10 July, but two were seen on 15 July. That date should have been a peak abundance day (Table 2). Frank Olsen and I surveyed on 13 July 2000 during peak flight time and counted two individuals.

A comparison of the closest single calendar date in the flight period eliminates the variable of Selby's more frequent surveys (Table

1). Note that Selby took two days to cover the site, hence the two dates. The later three years reflect a whole survey in a single day.

DISCUSSION

While there are differences in how the data were collected for each investigator and between investigators, the data were compelling. From Selby's (1988) first year to his second, he changed the number of transects from three to five in his unit 2. This could account for some of the increase from 1988 to 1989, but not for all of it. That is because the number of butterflies increased by 879% whereas the number of transects only increased by 66%. The 1995 survey followed Selby's transects throughout, but 1996 and 2000 were modified, in part, to spend more time in the critical habitat and not in the low, wet areas.

It can be inferred that there are tremendous annual variations in this population. Concern is here expressed that low populations, whether periodic or permanent, put this species at serious risk of extirpation. While we do not have pre-fire data, we do have data from early in the fire management regime for this site. If the current trend continues, little time remains to begin a recovery program because between the time grazing ended and the implementation of fire as a management tool began, the number of Arogos skipper individuals on Prairie Coteau has been in a precipitous decline. Grazing has been replaced by fire management, which certainly destroys nearly all invertebrates above ground. Metzler (1998) stated that "in Ohio, (as well as in the rest of the tall-grass prairie biome) fires for management purposes are used either in the early spring or late autumn following a hard frost, sometimes on an annual basis. Such use of fire does not mimic natural phenomena, thereby putting insects, which are vulnerable to fires, at risk." Therefore, the effect of fire must be examined closely in this decline.

Unpublished information forwarded by the Minnesota Department of Natural Resources showed that the critical native prairie area of the south unit (Selby's Unit 2) was partially burned in 1986, 1987, 1988, 1990, 1991 and 1995. It was also totally burned in 1993, 1997 and 1999. Surprisingly, (because it would seem that fire would be applied somewhat equally throughout the site), the adjacent east side (4S) unit was only burned in 1996. During that 14 years there was one accidental fire through the north end of the property and no natural fires even though lightning must have been present in an area of this size.

An illustration of the effect of the recent application of fire was evident in 2000. The south unit (Unit 2) where Selby had his highest counts was all burned in 29 September 1999. On 13 July 2000 it had many fewer prairie butterfly individuals than did the adjacent east unit (Selby's 4S unit). For example the south, most recently burned unit, had two Regal Fritillaries (*Speyeria idalia*) in 129 minutes of observation (0.015 individuals per minute), while the unburned east unit had 23 in 41 minutes of observation (0.56 individuals per minute), which is 37 times greater. There are no boundaries between the two units, and there appeared to be much more nectar available in the south unit.

Observations that butterfly populations are negatively impacted by fire are not new to this study. Arogos skipper populations are favored by idling, grazing and haying (Swengel 1997, Swengel and Swengel 1997, Swengel and Swengel 1999) and harmed by fire (Swengel 1996). The Dakota Skipper (*Hesperia dacotae*), another prairie species found on this site, has been shown to be negatively impacted by fire by Dana (1991) and has been lost from several sites under fire management, two of which are Cayler Prairie in Iowa and, after five continuous years of fire (1983–7), Pipestone Monument in Minnesota (Becker 1989).

Recommended management techniques that can be used to pre-

serve prairie invertebrate biodiversity have been discussed at various forums for the past decade (Dana 1991, Schlicht 1993, Hamilton 1994). Many of these techniques would lend themselves to the situation at Prairie Coteau. The data presented here suggest an urgency for their application.

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Thanks to Frank Olsen for providing his considerable observation skills that made the 2000 survey possible.

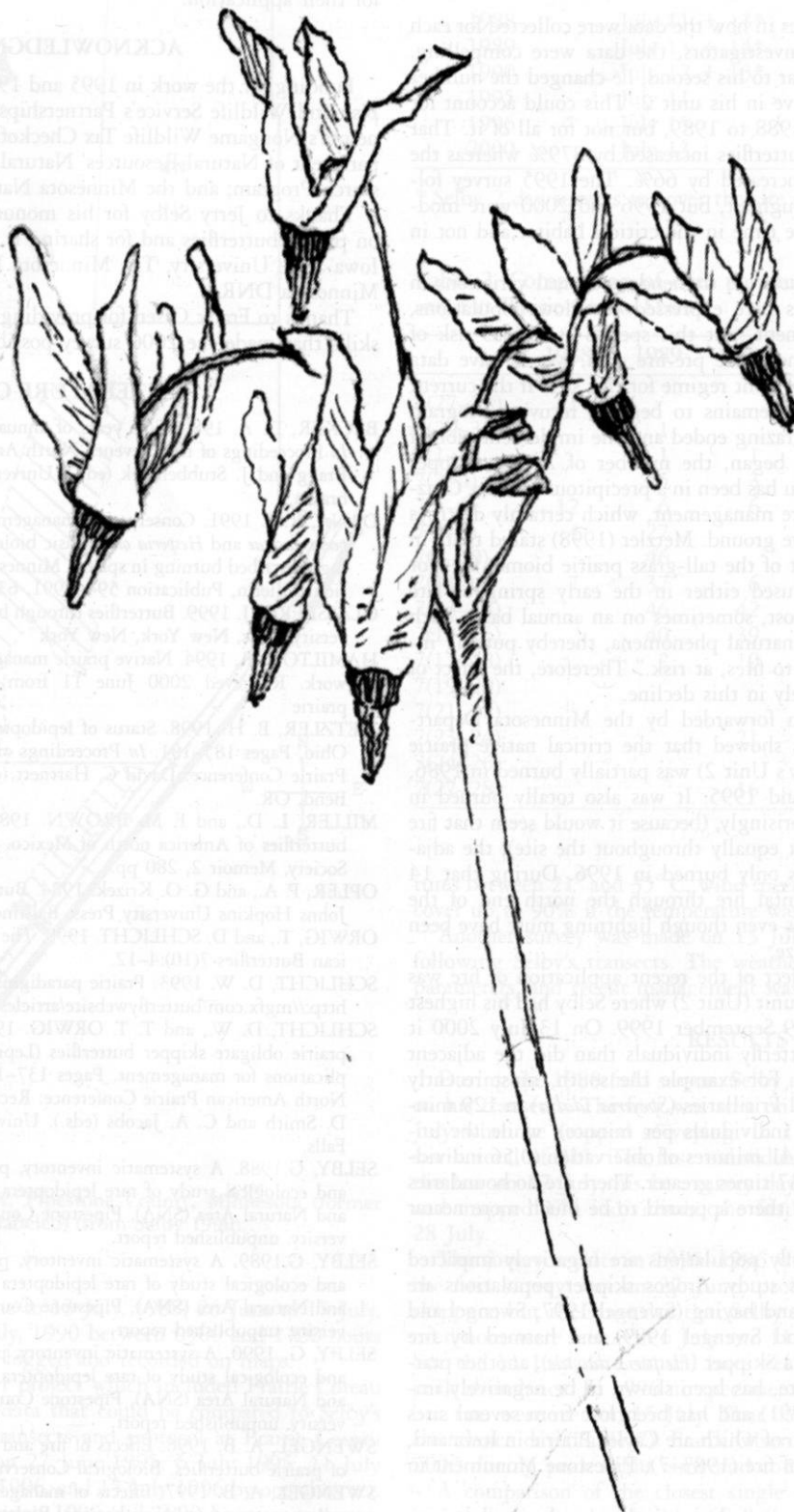
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A Comparison of Avian Communities Occupying Native and Exotic Grasslands in Kentucky: A Preliminary Study

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The diversity and abundance of grassland songbirds was examined in west-central Kentucky using point counts during June 1996 and 1997. Total bird abundance and species richness did not differ among three grassland habitats in 1996 or 1997. Grassland interior songbird abundance was higher in tall fescue (*Festuca arundinacea*) habitats compared to restored native warm-season grass and barrens habitats during both years of the study. Eastern Meadowlarks (*Sturnella magna*) and Henslow's Sparrows (*Ammodramus henslowii*) were most abundant in tall fescue fields. Red-winged Blackbirds (*Agelaius phoeniceus*) were more abundant in restored native warm-season grass than in barrens. Field Sparrows (*Spizella pusilla*), Common Yellowthroats (*Geothlypis trichas*) and Indigo Buntings (*Passerina cyanea*) were more abundant in barrens than in tall fescue fields. Restored native warm-season grass fields were smaller than barrens and tall fescue fields. Barrens had more woody stems than tall fescue and restored native warm-season grass fields. The presence and abundance of individual avian species appears to be largely dependent on field size and the amount of woody vegetation rather than the dominant grass species.

INDEX DESCRIPTORS: Kentucky, native warm-season grass, tall fescue, songbird.

At least 16 species of open grassland and savanna birds decreased over the past 25 years (Askins 1993) as the result of habitat loss from intensifying agriculture and succession on abandoned farms (Herkert 1991b, Rodenhouse et al. 1995, Herkert et al. 1996). Approximately 97% of the original tallgrass prairie has been destroyed in the midwestern United States and less than 2% of pre-settlement pine-grassland, oak barrens, and savanna communities remain in the southeastern and midwestern United States (Noss et al. 1995).

Tall fescue (*Festuca arundinacea*) may be the most commonly planted cool-season grass in the central and midwestern United States (Siegel et al. 1984). Over 14 million ha have been planted in the United States for livestock forage, Conservation Reserve Program (CRP) set aside grasslands, strip mine reclamation, and erosion control (Burns and Chamblee 1979). More than 97% of all tall fescue fields are infected with a symbiotic endophytic fungus (*Acremonium coenophialum*) (Siegel et al. 1984, Ball et al. 1993) which has a negative impact on the habitat, nutrition, and feeding preferences of several bird species (Madje and Clay 1991, Barnes et al. 1995, Barnes and Lane 1996, Conover and Messmer 1996a, Conover and Messmer 1996b).

Restored and naturally occurring grassland habitats (tallgrass prairie and barrens) dominated by native warm-season grasses also occur in Kentucky. Prior to European settlement, about 1.2 million ha of native warm-season grass prairie (barrens) existed in Kentucky (Transeau 1935). However, plowing, overgrazing, introduced forage species, and fire protection drastically reduced the amount of native prairie remaining in Kentucky. Today, less than 400 ha of remnant native warm-season grassland habitat, usually in patches less than 4 ha, remain in the state (Mark Evans, pers. comm.).

Previous research has documented avian abundance and richness in warm-season grass and cool-season grassland habitats in several midwestern states (George et al. 1979, Camp and Best 1993, Herkert 1994a, McCoy 1996, Best et al. 1997, Cooper 1997, Delisle and

Savidge 1997). Few studies, however, have compared avian abundance and richness between grasslands dominated by tall fescue and native warm-season grasses (McCoy 1996, Best et al. 1997, Cooper 1997). This study quantified and compared the abundance and species richness of songbirds in tall fescue, restored native warm-season grass, and remnant prairie barrens habitats.

METHODS

Study Sites

Eight sites, at least five ha each and idle from disturbance for two years, were selected for study in west-central and western Kentucky. Three CRP (tall fescue) fields, 22.4, 24.4, and 61.0 ha, were located in Hardin, Butler, and Boyle counties. Three restored native, warm-season grass fields, 6.5, 8.1, and 32.5 ha, were selected for study in Union and Boyle counties. Two remnant prairie barrens, 40.7 and 81.3 ha, were located on the Fort Campbell Military Reservation in Christian County. The rarity of restored native warm-season grass and barrens habitats in Kentucky prevented larger sample sizes.

Avian Surveys

Avian communities were surveyed using a fixed-radius point count technique (Hutto et al. 1986) during June 1996 and 1997. Survey locations within sites were randomly selected, were at least 200 m apart, and were at least 50 m from adjacent habitat types. Nine, 7, and 9 survey points were located in tall fescue, restored native warm-season grass, and barrens habitats, respectively. The number of points located in each field varied from one, in a small, restored native warm-season site, to five in large, barrens and tall fescue sites. The same points were visited each year. Ten-min counts were conducted at each location between 0630 and 0930 EST (Robbins 1981). Observer influence on bird detectability was reduced by allowing one min to elapse prior to initiating a count (Reynolds et al. 1980).

Birds were identified by sight, song, or call and recorded if they occurred within a 50 m radius circle (Hutto et al. 1986).

Points were surveyed once during 1996. Hutto et al. (1986) suggested that duplicating counts at a given point may be important when examining bird-habitat relationships. In addition, revisiting points may increase accuracy, as the phenology of singing may vary between species. Therefore, points were surveyed twice during 1997. The larger number of individuals of each species observed at each count location was used for analysis.

Vegetation Measurements

Plant communities were measured in four randomly placed 1 m² sampling quadrats located within 50 m of each count location, one in each cardinal direction (Oostings 1956). Percent vegetative cover and percent bare ground were visually estimated and plant species richness was measured in each sampling quadrat (Bonham 1989). The average height of vegetation was estimated at each sampling quadrat using visual obstruction methodology (Robel et al. 1970). In 1997, the number of woody stems was recorded by sampling a 10 m radius circular plot centered around each count location (Rauerson 1996).

Statistical Analyses

A test of association was used to determine if bird data from individual point counts should be analyzed or if counts from one site could be pooled for analysis (Ludwig and Reynolds 1988). All tests of association for 1996 and 1997 failed ($P > 0.05$) to reject the null hypothesis that point counts at the same site were independent (Larkin 1997). As a result, point counts were used as the source of replication for analyzing data. Separate analyses were conducted for 1996 and 1997 data.

Multiple Regression (SAS 1985) procedures were used to determine differences ($P < 0.05$) in avian abundance or species richness related to habitat type, field size, percent cover, percent bare ground, average plant height, plant species richness, and number of woody stems (not included in 1997 analysis). Vegetation data were analyzed using the GLM procedure (SAS 1985). Measurements for each vegetative characteristic taken at the four sampling quadrats at each point were averaged for statistical analysis. Fisher's Least Significance Difference (LSD) test ($P < 0.05$) was used to determine if differences in percent bare ground, percent cover, vegetative height, plant species richness, field size, number of woody stems, bird species richness, and bird abundance existed among habitat types.

Grassland bird species were placed into two habitat association categories: 1) interior and 2) edge (Palmer-Ball 1996) (Table 1). Habitat association and individual species-level data were analyzed using a nonparametric Kruskal-Wallis test for effects due to habitat type (Hollander and Wolfe 1973, Noether 1991, Baker and Lacki 1997). The NPAR1WAY procedure was utilized to generate these test statistics and probability values (SAS 1985). The Kruskal-Wallis test was used because species absence in some grassland habitat types resulted in zero values. This may have violated the assumption of the homogeneous variances which is critical for parametric statistics. Only species with a minimum of five detections per season were included in individual species analysis. If guild or individual species abundance differed ($P < 0.05$) among the three habitats, a distribution-free multiple comparison test based on the Kruskal-Wallis rank sums for large sample approximations was used to determine the specific habitats associated with the difference (Hollander and Wolfe 1973, Noether 1991, Baker and Lacki 1997). The IML procedure was utilized to calculate the appropriate test statistics and probability values for the multiple comparisons (SAS 1985). Noether (1991) suggested that when making multiple comparisons with an

Table 1. List of avian species observed during 1996 and 1997, and the habitat(s) in which each occurred. Species are listed in taxonomic order (American Ornithologist's Union 1998) and the number of observations for each species in tall fescue, restored native warm-season grass (R-NWSG) and barrens habitats are reported.

Common Name	Scientific Name	Fescue	R-NWSG	Barrens
Grassland Edge spp.^a				
Northern Bobwhite	<i>Colinus virginianus</i>	2	—	3
Yellow-billed Cuckoo	<i>Coccyzus americanus</i>	1	—	1
Eastern Phoebe	<i>Sayornis phoebe</i>	—	—	2
Eastern Kingbird	<i>Tyrannus tyrannus</i>	—	—	2
American Crow	<i>Corvus brachyrhynchos</i>	1	—	—
Tree Swallow	<i>Tachycineta bicolor</i>	3	—	—
Barn Swallow	<i>Hirundo rustica</i>	6	—	2
Eastern Bluebird	<i>Sialia sialis</i>	2	—	2
Northern Mockingbird	<i>Mimus polyglottos</i>	2	—	—
Prairie Warbler	<i>Dendrocica discolor</i>	—	—	4
Common Yellowthroat	<i>Geothlypis trichas</i>	—	3	10
Yellow-breasted Chat	<i>Icteria virens</i>	—	—	4
Chipping Sparrow	<i>Spizella passerina</i>	3	—	—
Field Sparrow	<i>Spizella pusilla</i>	—	11	19
Song Sparrow	<i>Melospiza melodia</i>	1	8	—
Northern Cardinal	<i>Cardinalis cardinalis</i>	—	2	2
Indigo Bunting	<i>Passerina cyanea</i>	—	10	9
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	14	29	—
Brown-headed Cowbird	<i>Molothrus ater</i>	3	3	1
American Goldfinch	<i>Carduelis tristis</i>	—	4	5
Grassland Interior				
Henslow's Sparrow	<i>Ammodramus benslowii</i>	22	—	—
Dickcissel	<i>Spiza americana</i>	2	—	—
Eastern Meadowlark	<i>Sturnella magna</i>	15	6	—

^a according to Palmer-Ball (1995).

experiment-wise error rate, an alpha larger than customarily used should be selected. Therefore, an alpha of 0.10 was used as the critical level in multiple comparison tests. Individual species analyses were performed on five species in 1996 and seven species in 1997.

RESULTS

A total of 220 birds representing 23 species was observed during the two years of this study (Table 1). There were no differences ($P > 0.05$) in total avian abundance or species richness due to habitat type, field size, percent cover, percent bare ground, average height, plant species richness, and abundance of woody vegetation for 1996 and 1997. Grassland interior songbird abundance was higher in fescue fields compared to restored native warm-season grass ($P = 0.01, 0.06$) and barrens ($P = 0.01, 0.001$) habitats in 1996 and 1997, respectively (Table 2).

Table 2. Number of observations for each bird species occurring in tall fescue, restored native warm-season grass (R-NWSG), and barrens habitats for species analyzed individually. (Note: Only species with a minimum of five detections per season were included in individual species analysis.)

Species/Guild	Fescue	R-NWSG	Barrens
1996	n = 8	n = 7	n = 9
Song Sparrow	1 ^a	4 ^a	0 ^a
Field Sparrow	0 ^a	6 ^a	9 ^a
Henslow's Sparrow	9 ^a	0 ^{ab}	0 ^b
Indigo Bunting	0 ^a	5 ^a	3 ^a
Red-winged Blackbird	4 ^a	11 ^a	0 ^a
Grassland Interior spp.	11 ^a	0 ^b	0 ^b
Grassland Edge spp.	6 ^a	26 ^b	16 ^{ab}
1997	n = 9	n = 7	n = 9
Common Yellowthroat	0 ^a	3 ^{ab}	10 ^b
Field Sparrow	0 ^a	5 ^{ab}	10 ^b
Henslow's Sparrow	13 ^a	0 ^b	0 ^b
Indigo Bunting	0 ^a	5 ^{ab}	6 ^b
Red-winged Blackbird	10 ^{ab}	18 ^a	0 ^b
Eastern Meadowlark	10 ^a	7 ^{ab}	0 ^b
Brown-headed Cowbird	3 ^a	3 ^a	0 ^a
Grassland Interior spp.	31 ^a	7 ^b	0 ^b
Grassland Edge spp.	30 ^a	43 ^a	50 ^a

^{ab} values within the same row with the same letters are not different at the $P = 0.05$ level.

Individual Species Analysis

There were no differences among habitats ($P > 0.10$) in bird abundance for four of five species analyzed in 1996 (Table 2). There were differences among habitats ($P < 0.10$) in bird abundance for six of the seven species analyzed in 1997.

Vegetation Characteristics

Fescue habitats were dominated by tall fescue. Other plants observed in this habitat included *Juniperus virginiana* (eastern red cedar), *Dactylis glomerata* (orchardgrass), *Trifolium pratense* (red clover), Cyperaceae (sedges), *Andropogon virginicus* (broomsedge), and *Erigeron* spp. (fleabanes). Restored native warm-season grass habitats were composed of several co-dominants including indiangrass, switch-

grass, little bluestem, and *Solidago* spp. (goldenrods). Other commonly observed plant species were broomsedge, *Rubus* spp. (blackberries), *Trifolium* spp. (clovers), fleabanes, *Phytolacca americana* (poke-weed), and *Stellaria* spp. (chickweed). Barrens habitats were dominated by several plant species including little bluestem, indiangrass, *Rubus* spp. (sumac), *Desmodium* spp. (desmodiums), goldenrods, *Eupatorium* spp. (eupatoriums), blackberries, and *Asclepias* spp. (milkweeds). The results of the vegetation analyses are presented in Table 3.

DISCUSSION

Size and successional condition of each study site may have had more influence on the presence of individual bird species than the species of grass dominating each habitat (native warm-season grass or tall fescue). Petit et al. (1995) and Cooper (1997) found that bird density increased with shrub density in open-land habitats. However, our results for overall avian abundance and species richness did not follow this trend. Barrens had more woody vegetation compared to tall fescue and restored native warm-season grass habitats (Table 3), however, barrens did not support more birds or species than restored native warm-season grass or tall fescue habitats. The smaller size and lower frequency of shrubs on our study sites may have been responsible for this difference (Petit et al. 1995, Cooper 1997).

The occurrence of some bird species appeared to be related to woody stem density. Scrub-shrub successional species such as the Prairie Warbler (*Dendroica discolor*), Field Sparrow, Common Yellowthroat, Yellow-billed Cuckoo (*Coccyzus americanus*), and Indigo Bunting were associated with barrens habitats with woody stem densities greater than 31 stems/10 m². In contrast, grassland interior specialists such as the Eastern Meadowlark, Henslow's Sparrow, and Dickcissel (*Spiza americana*) were associated with large, tall fescue fields having little or no woody vegetation (Table 3). These findings are consistent with other studies that have examined the effects of woody vegetation on interior grassland songbirds (Whitmore 1981, Zimmerman 1988, Herkert 1991a, Herkert 1994a, Herkert 1994b, Paterson and Best 1996).

Field size or habitat area has also been found to be critical for the use of grassland habitats by grassland interior songbirds (Samson 1980, Herkert 1991a, Herkert 1994b). With the exception of Field Sparrow, our data agree with this trend. However, this trend should be interpreted cautiously because of the low number of fields sampled in this study, resulting from the rarity of native warm-season grass sites in Kentucky.

Barrens were large enough (40.7 to 81.30 ha) to support grassland

Table 3. Means of percent cover, percent bare ground, plant species richness, average plant height, field size, and woody stems for tall fescue, restored native warm-season grass (R-NWSG), and barrens habitats in 1996 and 1997.

Habitat Type	N	% Cover		% Bare Ground		Spp. Richness		Average Plant Ht. (cm)		Field Size (ha)		Woody Stems	
		\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
1996													
Fescue	8	97 ^a	8.3	8 ^a	7.0	3.5 ^a	1.7	48 ^a	15.9	47 ^a	19.6	—	—
R-NWSG	7	95 ^a	9.6	15 ^a	21.3	6 ^b	1.4	72 ^b	15.8	25 ^b	12.3	—	—
Barrens	9	91 ^a	6.7	21 ^a	13.1	9 ^c	2.6	48 ^a	5.5	63 ^a	21.4	—	—
1997													
Fescue	9	90 ^a	12.6	17 ^b	13.4	4 ^a	1.3	56 ^a	10.1	44 ^a	19.8	15 ^a	25.1
R-NWSG	7	94 ^a	7.5	49 ^a	13.9	7 ^b	1.4	71 ^b	19.2	25 ^b	12.3	11 ^a	21.4
Barrens	8	89 ^a	14.3	25 ^b	19.9	9 ^c	1.3	51 ^a	16.0	61 ^a	21.7	182 ^b	149.4

^{abc} Means within the same column for the same year with the same letters are not different at the $P = 0.05$ level.

interior species, but contained too many woody stems to be used by most grassland interior songbirds (Table 3). Therefore, it was reasonable to find early successional scrub-shrub species such as Indigo Bunting, Common Yellowthroat, Prairie Warbler, and Field Sparrow. This observation stresses the importance of proper fire management for the few large tracts of created native warm-season grass and barrens habitats remaining in Kentucky and Tennessee if grassland interior songbird habitat is a management goal.

The restored native warm-season grass habitats examined in this study appeared structurally suitable for grassland interior birds (Table 3), but only one grassland interior species, the Eastern Meadowlark, was observed in this habitat type. Small field size most likely explains this finding. Restored native warm-season grass study sites ranged from 6.5 to 32.6 ha and were bordered primarily by fescue, row crop, forest, and scrub-shrub habitats. These sites were dominated by early successional scrub-shrub and grassland edge nesting birds such as Red-winged Blackbird, Field Sparrow, Common Yellowthroat, Indigo Bunting, and Song Sparrow. This observation is consistent with Herkert (1991a, 1991b) who found that smaller grasslands support few grassland interior species of birds and are dominated by non-interior grassland birds.

Tall fescue habitats met two of the most important habitat criteria for grassland interior songbirds because they were relatively large (22.35 to 60.98 ha) and had few woody stems (Table 3). Annual mowing which occurred up to two years prior to this study eliminated most woody vegetation, so more interior grassland species such as Eastern Meadowlark, Henslow's Sparrow, and Dickcissel were observed. Tall fescue may provide adequate nesting habitat for Eastern Meadowlark and Henslow's Sparrows despite Cooper's (1997) findings to the contrary. The fields studied by Cooper (1997) were mowed during the breeding season, whereas our fields remained uncut during the breeding season. Roseberry and Klimstra (1985) and Barnes et al. (1995) suggested tall fescue was poor habitat for Northern Bobwhite because dense growth inhibits their movements and eliminates foraging habitat. These factors are less problematic for grassland songbirds because they are smaller and more mobile than Northern Bobwhite. In addition, it is possible that dense growth of tall fescue fields may benefit grassland songbirds by making it more difficult for nest predators and parasites to locate nests.

Limited plant species diversity may compound the effects of low fescue nutrition on songbirds. The dense growth of tall fescue constrains plant diversity (Barnes et al. 1995). As a result of low plant diversity, songbirds may be forced to forage on nutrient deficient tall fescue due to the lack of other foods. Throughout this study, plant species richness was lowest in tall fescue habitats (Table 3). McCoy (1996) found plant diversity was lower in native warm-season grass fields compared to cool season grass fields; however, his native warm-season grass study sites were monocultures of switchgrass, whereas most of his cool-season grass study sites were mixed plantings. The barrens used in this study were botanically richer than the restored native warm-season grass fields. The relatively young age of the restored native warm-season grass fields, in addition to the species in the restored native warm-season grass planting mixture was most likely the reason for the difference in plant species richness between restored native warm-season grass and barrens habitats.

Diverse communities of Kentucky grassland birds may depend on both tall fescue and native warm-season grass habitats, at least until larger tracts of native warm-season grass habitats are established. While the results of this study may reflect the inadequacies of a small sample size rather than actual avian-habitat relations, it was a necessary first-step for understanding grassland songbird conservation in Kentucky. The potential for creating quality grassland interior songbird habitat in Kentucky is relatively great (i.e. reclaimed strip mines, wildlife management areas, and Conservation Reserve

Program lands); however, most landowners and the general public are unaware of or are unconcerned about grassland songbird needs. Once large tracts of native warm-season grass habitats are established, an in-depth study comparing the reproductive success of grassland songbirds inhabiting native warm-season grass versus tall fescue habitats will be essential for determining the importance of tall fescue habitats for grassland songbird conservation.

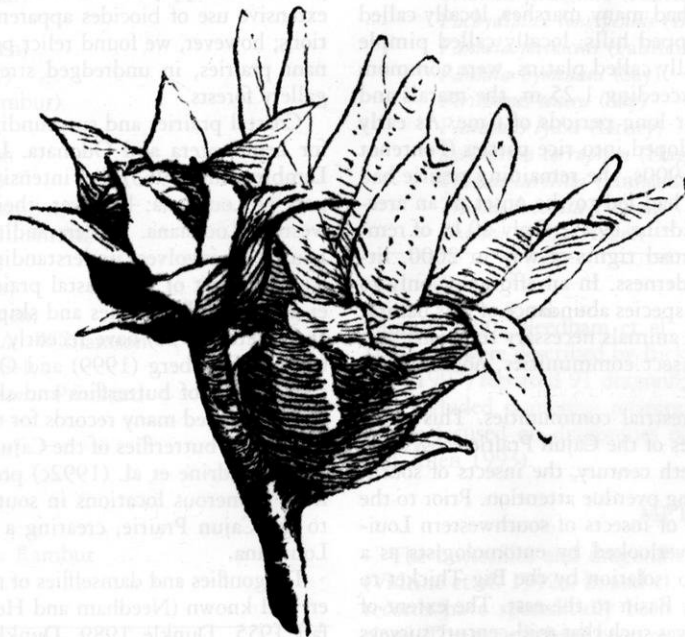
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Lepidopteran and Odonate Communities in the Cajun Prairie Ecosystem in Southwestern Louisiana

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Southwestern Louisiana has a poor record of insect studies. The region was generally overlooked by entomologists as a result of lack of accessibility due to isolation by the Big Thicket to the west and the Atchafalaya River Basin to the east. The prairie portion of southwestern Louisiana, known as Cajun Prairie, has been largely plowed for agriculture. The extent of damage was such that dragonfly and butterfly surveys of the mid-century ignored this ecosystem, considering it so impoverished as to have little native fauna remaining. In surveys of this ecosystem conducted from the late 1980s to the present, nearly 100 species each of Odonata and Lepidoptera were identified from the region. The long summers and brief winters extend the flight seasons and activities of the insects. Butterfly and dragonfly communities have apparently been decimated by the loss of suitable habitat and extensive use of biocides; however, relict populations of many species have been found on remnant prairies, in old-growth gallery forests, and in nearby habitats.

INDEX DESCRIPTORS: tallgrass prairie, Lepidoptera, butterflies, Odonata, dragonflies, Louisiana.

Southwestern Louisiana was once covered with lush tallgrass prairie vegetation (1 million ha) and associated swamps, marshes, pine forests with savannas and hillside bogs, bottomland hardwoods, and a little upland hardwood habitat. This prairie, the Cajun Prairie (Fig. 1), is the eastern extension of the Gulf coastal prairie (Allen and Vidrine 1989, Smeins et al. 1992, Vidrine et al. 1995, Allain and Johnson 1997, Allain et al. 1999). Numerous smaller prairies separated by streams and their gallery forests made up the Cajun Prairie. The prairie had many marshes, locally called marais, and small, often round-topped hills, locally called pimple mounds. Also, circular ponds, locally called platins, were common. With an average annual rainfall exceeding 1.25 m, the marais and platins were commonly flooded for long periods of time. As early as the late 1800s, these were developed into rice patties (Fontenot and Freeland 1976). By the mid-1900s, the remaining prairie had been plowed, and massive erosion had led to the onset of an area-wide stream-dredging program (Vidrine 1993). Only 40 ha of remnant prairies remained along railroad rights-of-way in 2000, literally the last vestiges of this wilderness. In an effort not only to census the biological diversity and species abundance of this habitat but also to discover the plants and animals necessary to reconstruct the habitat, descriptions of the insect communities, notably butterflies and dragonflies, were made.

Insects are key members of terrestrial communities. This paper centers on butterflies and dragonflies of the Cajun Prairie ecosystem. During the last half of the twentieth century, the insects of southwestern Louisiana received some long overdue attention. Prior to the mid-1900s, there were few studies of insects of southwestern Louisiana. The region was generally overlooked by entomologists as a result of lack of accessibility due to isolation by the Big Thicket to the west and the Atchafalaya River Basin to the east. The extent of damage resulting from agriculture was such that mid-century surveys

of Louisiana (Lambremont 1954, Bick 1957) considered the ecosystem so impoverished as to have little native fauna remaining. In contrast, we conducted surveys of this ecosystem mainly between 1986 and 1991. Nearly 100 species each of Odonata (dragonflies and damselflies) and Lepidoptera (butterflies and skippers) have been identified in the region. Long summers and brief winters extend the local flight seasons of the insects. The prairie plants provide a nearly year-round supply of nectar and pollen. Loss of suitable habitat and extensive use of biocides apparently decimated most insect populations; however, we found relict populations of many species on remnant prairies, in undredged streams, and in relatively old-growth gallery forests.

Coastal prairies and surrounding habitats have been surveyed for for Lepidoptera and Odonata. Lambremont (1954) and Ross and Lambremont (1963) did intensive surveys of butterflies and skippers of Louisiana; however, their works excluded most of southwestern Louisiana. Understanding the butterflies of southwestern Louisiana involves understanding the Cajun Prairie ecosystem, which is part of the coastal prairies of Texas and Louisiana (Allain et al. 1999). Butterflies and skippers of Texas (Neck 1996, Tveten and Tveten 1996) have recently been reviewed. Opler and Malikul (1998), Glassberg (1999) and Opler et al. (1995) provided recent species lists of butterflies and skippers for Louisiana, but none of these provided many records for the Cajun Prairie. A popular article focused on butterflies of the Cajun Prairie region (Allen and Vidrine 1990). Vidrine et al. (1992c) provided flight records of butterflies from numerous locations in southwestern Louisiana in or adjacent to the Cajun Prairie, creating a list of butterflies in southwestern Louisiana.

Dragonflies and damselflies of the southern United States are rather well known (Needham and Heywood 1929, Needham and Westfall 1955, Dunkle 1989, Dunkle 1990, Westfall and May 1996,

Table 1. Scientific names of dragonflies and damselflies of the Cajun Prairie ecosystem in southwestern Louisiana (Needham et al. 2000 and Vidrine et al. 1992b).

Odonata
Zygoptera
Calopterygidae
<i>Calopteryx dimidiata</i> Burmeister
<i>Calopteryx maculata</i> (Beauvois)
<i>Hetaerina titia</i> (Drury)
Lestidae
<i>Lestes disjunctus australis</i> Walker
<i>Lestes vigilax</i> Hagen in Selys
Coenagrionidae
<i>Argia apicalis</i> (Say)
<i>Argia fumipennis violacea</i> (Hagen)
<i>Argia moesta</i> (Hagen)
<i>Argia tibialis</i> (Rambur)
<i>Enallagma civile</i> (Hagen)
<i>Enallagma divagans</i> Selys
<i>Enallagma dubium</i> Root
<i>Enallagma durum</i> (Hagen)
<i>Enallagma exsulans</i> (Hagen)
<i>Enallagma geminatum</i> Kellicott
<i>Enallagma signatum</i> (Hagen)
<i>Enallagma traviatum westfalli</i> Donnelly
<i>Ischnura (Anomalagrion) hastata</i> (Say)
<i>Ischnura posita</i> Hagen
<i>Ischnura prognata</i> Hagen
<i>Ischnura ramburii</i> (Selys)
<i>Nehalennia integrollis</i> Calvert
<i>Telebasis byersi</i> Westfall
Anisoptera
Petaluridae
<i>Tachopteryx thoreyi</i> (Hagen)
Aeshnidae
<i>Anax junius</i> (Drury)
<i>Basiaeschna janata</i> (Say)
<i>Boyeria vinosa</i> (Say)
<i>Coryphaeschna ingens</i> (Rambur)
<i>Epiaeschna heros</i> (Fabricius)
<i>Gomphaeschna antilope</i> (Hagen)
<i>Gomphaeschna furcillata</i> (Say)
<i>Nasiaeschna pentacantha</i> (Rambur)
Gomphidae
<i>Aphylla angustifolia</i> Garrison
<i>Aphylla williamsoni</i> (Gloyd)
<i>Arigomphus maxwelli</i> (Ferguson)
<i>Arigomphus submedianus</i> (Williamson)
<i>Dromogomphus armatus</i> Selys
<i>Dromogomphus spinosus</i> (Selys)
<i>Dromogomphus spoliatus</i> (Hagen)
<i>Gomphus (Gomphorus) hybridus</i> Williamson
<i>Gomphus (Gomphus) lividus</i> Selys
<i>Gomphus (Gomphus) oklahomensis</i> Pritchard
<i>Hagenius brevistylis</i> Selys
<i>Progomphus obscurus</i> (Rambur)
<i>Stylurus laurae</i> (Williamson)
<i>Stylurus plagiatus</i> (Selys)
Cordulegastridae
<i>Cordulegaster obliqua fasciata</i> Rambur
Libellulidae
Macromiinae

Table 1. Continued.

<i>Didymops transversa</i> (Say)
<i>Macromia illinoiensis georgina</i> (Selys)
<i>Macromia taeniolata</i> Rambur
Corduliinae
<i>Epicordulia princeps</i> Hagen
<i>Helocordulia selysii</i> (Hagen)
<i>Neurocordulia alabamensis</i> Hodges
<i>Neurocordulia molesta</i> (Walsh)
<i>Neurocordulia obsoleta</i> (Say)
<i>Somatochlora filosa</i> (Hagen)
<i>Somatochlora georgiana</i> Walker
<i>Somatochlora linearis</i> (Hagen)
<i>Tetragoneuria cynosura</i> (Say)
Libellulinae
<i>Brachymesia grvida</i> (Calvert)
<i>Celithemis amanda</i> (Hagen)
<i>Celithemis berthia</i> Williamson
<i>Celithemis elisa</i> (Hagen)
<i>Celithemis eponina</i> (Drury)
<i>Celithemis fasciata</i> Kirby
<i>Celithemis omata</i> (Rambur)
<i>Celithemis vema</i> Pritchard
<i>Erythemis simplicicollis</i> (Say)
<i>Erythrodiplax berenice berenice</i> (Drury)
<i>Erythrodiplax miniscula</i> (Rambur)
<i>Ladona deplanata</i> Rambur
<i>Libellula auripennis</i> Burmeister
<i>Libellula axilena</i> Westwood
<i>Libellula cyanea</i> Fabricius
<i>Libellula flavida</i> Rambur
<i>Libellula incesta</i> Hagen
<i>Libellula luctuosa</i> Burmeister
<i>Libellula needhami</i> Westfall
<i>Libellula semifasciata</i> Burmeister
<i>Libellula vibrans</i> Fabricius
<i>Macrodiplax balteata</i> (Hagen)
<i>Miathyria marcella</i> (Selys in Sagra)
<i>Orthemis ferruginea</i> (Fabricius)
<i>Pachydiplax longipennis</i> (Burmeister)
<i>Pantala flavescens</i> (Fabricius)
<i>Pantala hymenaea</i> (Say)
<i>Perithemis tenera</i> (Say)
<i>Plathemis lydia</i> (Drury)
<i>Sympetrum corruptum</i> (Hagen)
<i>Tramea carolina</i> (Linnaeus)
<i>Tramea lacerata</i> Hagen
<i>Tramea onusta</i> Hagen

Dunkle 2000, Needham et al. 2000). Those species that occur in Louisiana were described by Bick (1957) and Mauffray (1997). Mauffray (1997) reported 91 dragonflies and 33 damselflies from the state and included numerous references to the Cajun Prairie. A popular article focused on dragonflies of the Cajun Prairie region (Vidrine and Allen 1993).

METHODS

The butterflies and dragonflies were monitored from 1986–1991 (Vidrine et al. 1992a, b, and c). Since these records, additional sight records have sporadically been noted, especially in prairie restorations. The records have been re-evaluated using recent work by other

Table 2. Scientific and common names of butterflies of the Cajun Prairie ecosystem (adapted from Vidrine et al. 1992c, Opler and Malikul 1998, and Glassberg 1999). Common names are provided as they are rather standardized for butterflies. The skippers are omitted in this paper for two reasons: sight identifications of adults are difficult for many species, and our data are limited on this group. However, the web site (Opler et al. 1995) and books (Opler and Malikul 1998 and Glassberg 1999) detail much of what is known about Louisiana skippers. Two books for Texas butterflies list species from the coastal prairie, which extends to Louisiana as the Cajun Prairie (Neck 1996, Tveten and Tveten 1996).

Lepidoptera	
Papilionidae	
Papilioninae	
<i>Battus philenor</i> (Linnaeus)	pipevine swallowtail
<i>Eurytides marcellus</i> (Cramer)	zebra swallowtail
<i>Papilio polyxenes</i> Stoll	black swallowtail
<i>Papilio cressphontes</i> Cramer	giant swallowtail
<i>Papilio glaucus</i> (Linnaeus)	eastern tiger swallowtail
<i>Papilio troilus</i> Smith	spicebush swallowtail
<i>Papilio palamedes</i> Drury	palamedes swallowtail
Pierinae	
<i>Anthocharis midea</i> (Huebner)	falcate orangetip
<i>Pontia protodice</i> (Boisduval and Leconte)	checkered white
Coliadinae	
<i>Colias eurytheme</i> Boisduval	orange sulphur
<i>Colias cesonja</i> (Stoll)	southern dogface
<i>Eurema daira</i> (Latrielle)	barred yellow
<i>Eurema lisa</i> (Boisduval and Leconte)	little sulphur
<i>Eurema nicippe</i> (Cramer)	sleepy orange
<i>Phoebis sennae</i> (Linnaeus)	cloudless sulphur
Lycaenidae	
Theclinae	
<i>Atlides halesus</i> (Cramer)	great purple hairstreak
<i>Callophrys nippon</i> (Huebner)	eastern pine elfin
<i>Calycopis cecrops</i> (Fabricius)	red-banded hairstreak
<i>Parrhasius m-album</i> (Boisduval and Leconte)	white-M hairstreak
<i>Satyrrium calanus</i> (Huebner)	banded hairstreak
<i>Satyrrium liparops</i> (Leconte)	striped hairstreak
<i>Strymon melinus</i> (Huebner)	gray hairstreak
Polyommatainae	
<i>Celastrina ladon</i> (Cramer)	spring azure
<i>Celastrina neglecta</i> Opler and Krized	summer azure
<i>Everes comyntas</i> (Godart)	eastern tailed-blue
Riodinidae	
<i>Calephelis virginienis</i> (Guerlin)	little metalmark
Nymphalidae	
Libytheinae	
<i>Libytheana carinenta</i> (Cramer)	American snout
Heliconiinae	
<i>Agraulis vanillae</i> (Linnaeus)	Gulf fritillary
<i>Dryas julia</i> (Fabricius)	Julia
<i>Euptoieta claudia</i> (Cramer)	variegated fritillary
<i>Heliconius charithonius</i> (Linnaeus)	zebra
Nymphalinae	
<i>Chlosyne gorgone</i> (Huebner)	gorgone checkerspot
<i>Junonia coenia</i> (Huebner)	common buckeye
<i>Phycoides phaon</i> (Edwards)	phaon crescent
<i>Phycoides texana</i> (Edwards)	Texan crescent
<i>Phycoides tharos</i> (Drury)	pearl crescent
<i>Polygonia interrogationis</i> (Fabricius)	question mark
<i>Polygonia comma</i> (Harris)	eastern comma
<i>Vanessa atalanta</i> (Linnaeus)	red admiral
<i>Vanessa cardui</i> (Linnaeus)	painted lady
<i>Vanessa virginiensis</i> (Drury)	American lady
Limnitiidinae	
<i>Limnitis archippus</i> (dos Passos)	viceroxy
<i>Limnitis arthemis</i> (Fabricius)	red-spotted purple

Table 2. Continued.

Charaxinae	
<i>Anaea andria</i> (Scudder)	goatweed leafwing
Apaturinae	
<i>Asterocampa celtis</i> (Edwards)	hackberry emperor
<i>Asterocampa clyton</i> (Boisduval and Leconte)	tawny emperor
Satyrinae	
<i>Cercyonis pegala</i> (Fabricius)	common wood-nymph
<i>Cyllopsis gemma</i> (Huebner)	gemmed satyr
<i>Enodia creola</i> (Skinner)	Creole pearly-eye
<i>Enodia portlandica</i> (Fabricius)	southern pearly-eye
<i>Hermeuptychia sosybius</i> (Fabricius)	Carolina satyr
<i>Megisto cymela</i> (Cramer)	little wood satyr
<i>Neonympha areolata</i> (Smith)	Georgia satyr
Danainae	
<i>Danaus gilippus</i> (Cramer)	queen
<i>Danaus plexippus</i> (Linnaeus)	monarch

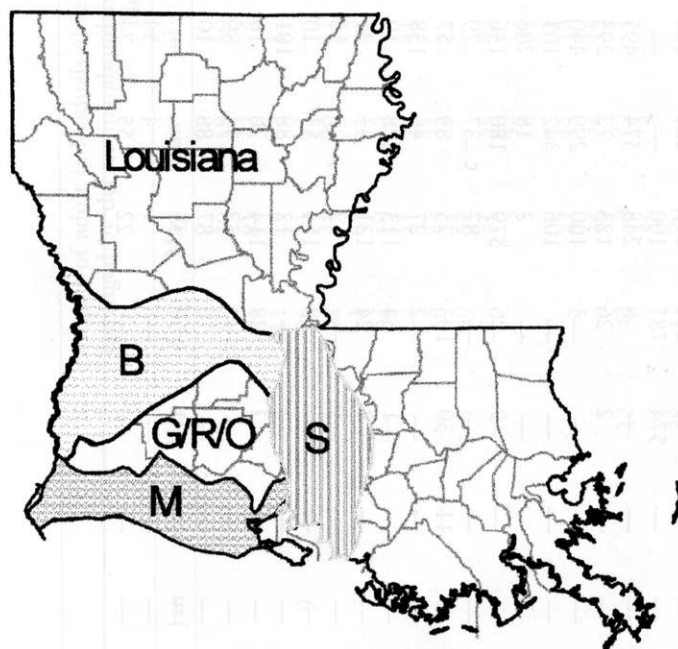


Fig. 1. The map depicts the state of Louisiana and varied habitats in southwestern Louisiana. Southwestern Louisiana was once considered a great prairie, but it actually was tallgrass prairie divided into smaller prairies by gallery (riverine) forests. The prairies also graded into savannas with pine forests, marshes, and bottomland hardwood forests. The primary habitats are located on the map using varied shadings and uppercase letters. The location symbols include: B (bogs, baygalls, savannas, pine woodland), G (gallery forests and streams), M (fresh, brackish and salt marshes), O (open agricultural land, usually rice and soybean fields), R (remnant and restored prairie and marais), and S (freshwater swamp and bottomland hardwood forest). The historical prairie is represented by the region labelled by G, R, and O. Numerous ecotones exist, and habitat alteration masks delineation zones of the varied habitats. Sampling stations were scattered throughout the Cajun Prairie region encompassing southwestern Louisiana.

collectors and authors. More than 100 stations in varied habitats associated with the Cajun Prairie ecosystem were routinely visited by Vidrine, usually once or twice per month, between 1986 and 1991. As such, a total of 2,487 stations were visited. Each station involved a 30-minute visit in which all observed adult dragonflies and butterflies were identified and counted, constituting flight/sight records. These data are tabulated and presented in the Results section. A map (Fig. 1) shows the Cajun Prairie region and roughly delineates the varied habitat types sampled.

RESULTS

Between 1986 and 1991, we observed 73,742 adult odonates and 8,517 adult butterflies (skippers excluded) (Vidrine et al. 1992b, c). Based upon our records and those listed by Mauffray (1997), 92 species of dragonflies and damselflies occur in the Cajun Prairie ecosystem (Table 1). The state list has 91 dragonflies and 33 damselflies for a total of 124 species of odonates in Louisiana. Based upon our records and those listed in Opler et al. (1995), 54 species of butterflies occur in the Cajun Prairie ecosystem (Table 2). Their state list has 79 butterflies and 58 skippers for a total of 137 species. The names have been updated to match the currently accepted nomenclature.

Flight and flight location preference records are provided in Tables 3 and 4. Records for species determined to be overly difficult to separate as sight records are combined into species groups. Relative numbers of individuals and seasonal adult activity are readily perceived from the tables. The tables also list habitat preferences based upon the locations of most of the flight records for each species. Most of these adult insects either prefer the prairie region or commonly visit the region, although larval development may occur in other habitats.

DISCUSSION

The primary purpose of this paper is to list the dragonflies and butterflies of the Cajun Prairie ecosystem in southwestern Louisiana. The search for remnant prairies led to a similar search for populations of native insects, mainly butterflies and dragonflies. The results of these searches include 92 species of Odonata (dragonflies and damselflies) and 54 Lepidoptera (butterflies, excluding skippers and moths) in the prairie ecosystem and associated habitats. The region contains a diverse assemblage of these insects; however, many species are locally abundant and/or extremely rare based upon our sampling.

Table 3. Flight records and preferred locations of dragonflies from the Cajun Prairie ecosystem in southwestern Louisiana. The records are sight records collected during 1986-1991 (Vidrine et al. 1992b). A total of 76 species/species groups made up 73,742 sightings at 2,487 stations. Totals of monthly sightings and preferred locations of each odonate species are provided. Location symbols: A (no preference), B (bogs, baygalls, savannas, pine woodland), G (gallery forests and streams), M (fresh, brackish and salt marshes), O (open agricultural land, usually rice and soybean fields), R (remnant and restored prairie and marais), and S (freshwater swamp and bottomland hardwood forest).

Dragonflies	Number of adult individuals observed (arranged by decreasing abundance)												Total	Location
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec		
<i>Pachydiplax longipennis</i>	—	—	81	1465	4161	2579	2995	2476	759	424	21	1	14962	A
<i>Erythemis simplicicollis</i>	—	—	28	787	2858	2393	2032	1188	753	488	29	—	10536	A
<i>Celithemis eponina</i>	—	—	—	6	942	2227	1734	786	64	4	—	—	5763	ROGM
<i>Anax junius</i>	18	4	70	283	478	392	692	1174	905	739	184	89	5028	A
<i>Brachymesia gravida</i>	—	—	—	—	445	1521	931	568	147	7	—	—	3619	ROM
<i>Argia tibialis</i>	—	—	30	1065	1358	630	134	235	105	11	4	—	3572	A
<i>Pantala flavescens</i>	—	1	—	—	3	67	941	1137	648	486	112	20	3415	A
<i>Libellula needhami/auripennis</i>	—	—	—	4	921	1253	652	387	3	—	—	—	3220	A
<i>Perithemis tenera</i>	—	—	—	104	523	479	612	379	378	104	11	—	2590	A
<i>Pantala hymenaea</i>	—	—	1	53	273	1190	542	186	5	—	—	—	2250	A
<i>Ischnura (A.) bastata</i>	—	69	260	541	236	232	119	272	26	42	30	1	1855	A
<i>Platbemis lydia</i>	—	—	30	226	259	221	568	376	124	34	1	—	1839	A
<i>Tetragoneuria cynosura</i>	—	—	574	781	100	—	—	—	—	—	—	—	1455	A
<i>Libellula vibrans</i>	—	—	—	8	248	374	495	276	18	—	—	—	1419	GBS
<i>Tramea lacerata/onista</i>	—	—	2	26	123	72	293	334	248	133	6	4	1241	A
<i>Libellula incesta</i>	—	—	—	3	100	299	440	308	37	1	—	—	1188	GB
<i>Erythrodiplax berenice berenice</i>	—	—	—	—	106	342	105	515	6	1	—	—	1075	M
<i>Orthemis ferruginea</i>	7	—	—	—	2	18	206	244	141	165	101	44	928	ROGB
<i>Calopteryx maculata</i>	—	—	2	26	379	180	136	56	35	28	—	—	842	GB
<i>Argia moesta</i>	—	—	—	—	87	37	79	276	76	8	—	—	563	G
<i>Ischnura ramburii</i>	—	11	30	103	75	89	57	89	29	47	13	4	547	A
<i>Tramea carolina</i>	—	—	—	2	27	46	138	126	46	16	—	—	401	A
<i>Coryphaeschna ingens</i>	—	—	1	34	113	228	19	3	2	—	—	—	400	A
<i>Erythrodiplax miniscalca</i>	—	—	2	24	121	33	25	84	12	14	10	—	325	ROGB
<i>Hetaerina titia</i>	—	—	—	—	8	27	56	60	67	84	14	—	320	GB
<i>Argia apicalis</i>	—	—	—	—	12	53	10	14	16	7	1	—	263	ROGB
<i>Aphylla angustifolia</i>	—	—	—	—	12	88	101	34	3	—	—	—	238	RO
<i>Epiaeschna heros</i>	—	—	2	28	114	70	16	14	1	—	—	—	235	A
<i>Libellula flavida</i>	—	—	—	2	32	54	89	43	2	—	—	—	222	B
<i>Arigomphus submedianus/maxwelli</i>	—	—	—	16	87	88	10	—	—	—	—	—	201	GR
<i>Ladona deplanata</i>	—	—	101	58	35	—	—	—	—	—	—	—	194	G
<i>Macrodiplox baltata</i>	—	—	—	—	1	4	54	131	1	1	—	—	192	GRM
<i>Epicordulia princeps</i>	—	—	—	—	22	55	74	37	—	—	—	—	188	ROG

Table 3. Continued.

Dragonflies	Number of adult individuals observed (arranged by decreasing abundance)												Total	Location
	Months													
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec		
<i>Celithemis fasciata</i>	—	—	—	63	30	18	50	3	—	—	—	—	164	B
<i>Libellula semifasciata</i>	—	—	4	41	81	32	4	1	—	—	—	—	162	B
<i>Enallagma civile</i>	—	—	4	11	19	82	12	14	7	1	1	—	151	A
<i>Sympetrum corruptum</i>	9	—	23	26	1	13	—	—	—	12	49	14	147	ROG
<i>Ischnura posita</i>	—	—	15	12	43	20	11	10	3	4	1	—	119	A
<i>Lestes vigilax</i>	—	—	—	1	61	11	32	2	4	5	—	—	116	ROG
<i>Celithemis verna</i>	—	—	—	94	19	2	—	—	—	—	—	—	115	B
<i>Somatochlora linearis</i>	—	—	—	—	31	26	41	15	—	—	—	—	113	GB
<i>Calopteryx dimidiata</i>	—	—	—	30	43	33	—	—	—	—	—	—	107	GB
<i>Enallagma divagans</i>	—	—	5	49	52	—	—	—	—	—	—	—	106	B
<i>Progomphus obscurus</i>	—	—	—	—	25	25	22	24	—	—	—	—	96	GB
<i>Celithemis amanda</i>	—	—	—	—	2	24	37	26	—	—	—	—	89	B
<i>Miathyria marcella</i>	—	—	—	—	—	—	1	54	26	6	—	—	87	GR
<i>Dromogomphus spinosus</i>	—	—	—	—	41	33	10	2	—	—	—	—	86	GR
<i>Nasiaeschna pentacantha</i>	—	—	1	4	36	24	15	3	—	—	—	—	83	GS
<i>Enallagma signatum</i>	—	—	22	42	2	12	1	—	—	—	—	—	79	GB
<i>Telebasis byersi</i>	—	—	—	—	58	4	—	—	—	—	—	—	62	GSB
<i>Gomphus lividus</i>	—	—	28	13	20	—	—	—	—	—	—	—	61	BG
<i>Celithemis elisa</i>	—	—	—	6	21	16	4	9	—	—	—	—	56	RB
<i>Enallagma spp.</i>	—	—	—	8	31	—	2	9	1	2	1	—	54	GB
<i>Boyeria vinosa</i>	—	—	—	—	1	1	8	8	19	14	—	—	51	GSB
<i>Macromia illinoensis georgina</i>	—	—	—	—	9	7	12	18	5	—	—	—	51	GB
<i>Argia fumipennis violacea</i>	—	—	—	7	18	7	8	2	2	3	—	—	47	B
<i>Gomphus hybridus/modestus</i>	—	—	2	31	9	3	—	—	—	—	—	—	45	GB
<i>Gomphus oklabomensis</i>	—	—	18	21	2	—	—	—	—	—	—	—	41	GB
<i>Lestes disjunctus australis</i>	1	5	5	13	7	—	—	—	2	5	—	—	38	RGB
<i>Dromogomphus spoliatus</i>	—	—	—	—	—	5	9	21	1	—	—	—	36	GB
<i>Hagenius brevistylis</i>	—	—	—	—	—	20	5	8	1	—	—	—	34	GSB
<i>Aphylla williamsoni</i>	—	—	—	—	—	—	8	20	6	—	—	—	34	GB
<i>Lestes inaequalis</i>	—	—	—	—	26	7	—	—	—	—	—	—	33	GB
<i>Tachopteryx thoreyi</i>	—	—	—	1	7	14	7	—	—	—	—	—	29	B
<i>Didymops transversa</i>	—	—	9	13	4	—	—	—	—	—	—	—	26	B
<i>Macromia taeniolata</i>	—	—	—	—	1	14	3	2	2	—	—	—	22	GB
<i>Libellula luctuosa</i>	—	—	—	—	2	1	13	4	—	—	—	—	20	GB
<i>Stylurus plagiatus</i>	—	—	—	—	—	—	3	6	8	—	—	—	17	B
<i>Celithemis omata</i>	—	—	—	3	10	2	—	—	—	—	—	—	15	B
<i>Celithemis bertba</i>	—	—	—	2	10	3	—	—	—	—	—	—	15	B
<i>Cordulegaster obliqua fasciata</i>	—	—	—	—	6	1	1	—	—	—	—	—	8	B
<i>Neurocordulia molesta</i>	—	—	—	—	3	1	1	2	—	—	—	—	7	G
<i>Libellula cyanea</i>	—	—	—	—	1	1	—	—	—	—	—	—	2	B
<i>Stylurus laurae</i>	—	—	—	—	2	—	—	—	—	—	—	—	2	B
<i>Helocordulia selysii</i>	—	—	—	1	—	—	—	—	—	—	—	—	1	B
<i>Somatochlora filosa</i>	—	—	—	—	—	—	—	1	—	—	—	—	1	B

Table 4. Continued.

Butterflies	Number of adult individuals observed (arranged by decreasing abundance) Months												Total	Location	
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec			
<i>Danaus gilippus</i>	—	—	—	—	—	—	2	1	—	—	—	—	—	3	RB
<i>Satyrus liparops</i>	—	—	—	—	1	—	—	—	—	—	—	—	—	2	G
<i>Atides batesus</i>	—	—	—	—	—	—	—	—	1	—	—	—	—	2	B
<i>Celastrina ladoni/neglecta</i>	—	—	—	1	—	—	—	—	—	—	—	—	—	2	G
<i>Calphobeta virginensis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	1	B
<i>Calliope niphon</i>	—	—	1	—	—	—	—	—	—	—	—	—	—	1	B
<i>Parrhasius m-album</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	1	S

The long summers and brief winters extend the flight seasons and activities of the insects. Prairie remnants and prairie restorations provide a nearly year-round source of nectar and pollen resources. Loss of suitable habitat and extensive use of biocides have apparently decimated most insect populations; however, relict populations of many species have been found on remnant prairies, in undredged streams, and in relatively old-growth gallery forests.

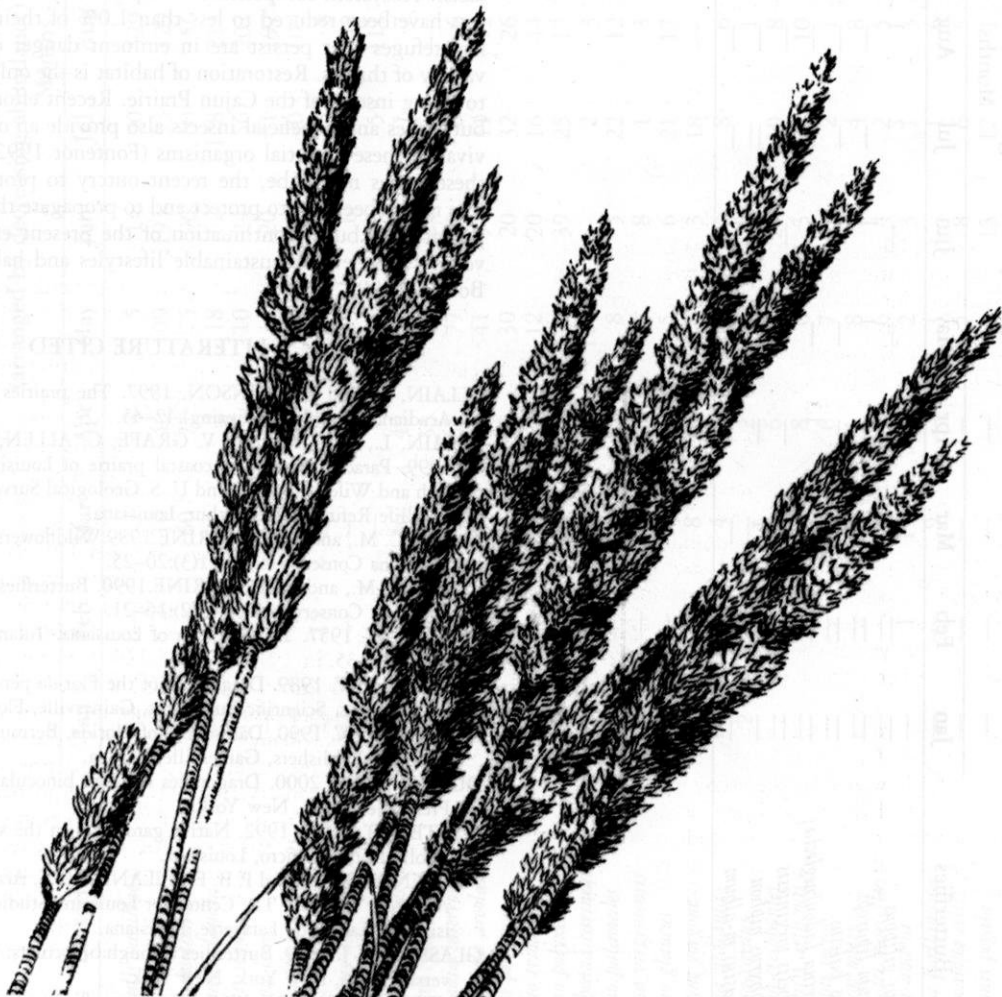
Relict populations persist for a number of species of butterflies and dragonflies in southwestern Louisiana. The continuing threats to these populations by urbanization, intense sedimentation from not only urban runoff but also from the continuous activities of farmers employing extensive plowing, and intense and continuous applications of massive amounts of biocides to massive monocultures of rice, soybean, and turf grass are evident. Some relict populations of butterflies have survived on small plots of native wildflowers with minimal sources of nectar and safe harbor from insecticides. The rice fields and drainage canals have provided habitat for many common species of dragonflies and damselflies, but the dredging of streams and the leveling of marshes and other wet habitats have robbed rarer species of suitable habitat. Many of these insects survive on the periphery of the prairie.

Restoration of habitat is essential. The Cajun Prairie and its adjacent ecosystem components exemplified by streams and gallery forests have been reduced to less than 1.0% of their original area. The few refuges that persist are in eminent danger of eradication by a variety of threats. Restoration of habitat is the only recourse available to flying insects of the Cajun Prairie. Recent efforts at gardening for butterflies and beneficial insects also provide an opportunity for survival of these essential organisms (Fontenot 1992). As important as these issues might be, the recent outcry to protect the pollinators like native bees and to protect and to propagate the variety of natural predators is but a continuation of the present effort to protect diversity and develop sustainable lifestyles and habitats (Vidrine and Borsari 1999).

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Ada Hayden: Champion of Iowa Prairies

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Ada Hayden developed a love for prairies during her childhood. She was born in 1884 on a farm just north of Ames, Iowa, where her father had left several acres of prairie and wetland unplowed. While in her teens, she came under the influence of Louis H. Pammel, whose work in conservation was a model and inspiration during the many years he was her mentor. Ada Hayden chose prairies as the subject of her earliest research; her Ph.D. dissertation was on the anatomical adaptations of prairie plant species. Two journal papers based on her dissertation and two additional publications on prairies were in print within a year of awarding of her degree. After receiving her doctorate at Iowa State College, she was employed there as Assistant Professor of Botany, later as Research Assistant Professor of the Agricultural Experiment Station and Curator of the Herbarium. Almost single-handedly she pioneered the idea of setting aside prairie remnants in Iowa as state-owned preserves. Her field work culminated in a summary paper in 1947 describing 22 prairie areas worthy of preservation. She convincingly argued that these tracts should be given the highest priority for state purchase and preservation. She promoted her ideas in professional organizations and spoke of her cause in many venues. Her writings, including both technical publications and semi- or non-technical, descriptive articles, also helped stir public support for conservation of the state's remaining natural areas. Iowa's state preserves and the State Preserves Advisory Board are direct legacies of her efforts. Her work provides an example of dedication and perseverance for today's conservationists and natural historians.

INDEX DESCRIPTORS: Ada Hayden; prairie; conservation; preserves; Ames, Iowa.

Ada Hayden was born in the vicinity of Ames, Iowa, on 14 August 1884. Her parents, David Maitland Hayden and Christina Shearer Hayden, owned an 80-acre farm "3 miles northwest of Ames," a description which was later included on numerous herbarium specimen labels. The location of this property was T84N, R24W (Franklin Twp.), E $\frac{1}{2}$, NW $\frac{1}{4}$, Sec. 27 (unpubl. records, Auditor's Office, Story County). Her maternal grandparents, Mr. and Mrs. Robert Bruce Shearer, were early pioneers in Story County (Anonymous 1950), and, until 1902, they owned a farm adjacent to the Hayden property.

Ada's family's land was apparently quite variable in terrain, from gravelly prairie knolls with *Pulsatilla patens* (L.) P. Miller (pasque flowers) and *Astragalus crassicaarpus* Nutt. (ground plums) to wet spots with *Caltha palustris* L. (marsh marigolds) and *Cypripedium candidum* Muhl. (small white lady's-slipper orchids), as documented by specimens in Iowa State University's Ada Hayden Herbarium. The farm was Ada's playground in her youth and her sanctuary as she grew older. It also helped create her love of natural areas from an early age.

By the time she graduated from Ames High School, she had made the acquaintance of Iowa State College botanist Louis Pammel (Isely 1989). Her love of plants drew her to the study of botany at the college, and she chose Pammel as her advisor. She graduated from Iowa State in 1908, having been an honors student, a basketball player, and a member of several college organizations (Lovell 1987; unpubl. records, Iowa State University Library, Special Collections Department).

She soon began study at Washington University in Saint Louis, where she obtained her Master's degree in 1910. She then returned to Ames that year to begin work on a second Master's degree (received 1911), then her Ph.D. at Iowa State (awarded 1918).

INITIATION OF HER PRAIRIE RESEARCH AND PUBLICATION

Ada Hayden's research on prairies apparently started soon after her return to Ames (Fig. 1). In 1911, she had an abstract about types of prairies published in the *Proceedings of the Iowa Academy of Science* (Hayden 1911). In 1919, two papers resulting from her dissertation on the "ecologic anatomy" of several prairie plant species were published in the *American Journal of Botany* (Hayden 1919a, 1919b). The same year, an expanded paper based on the 1911 abstract was published in the *Proceedings of the Iowa Academy of Science* (Hayden 1919c).

Also that year she wrote a paper for the *Iowa Parks* report to the State Board of Conservation on the need to initiate efforts to set aside prairie areas as preserves (Hayden 1919d). In 1917 the state legislature had authorized the creation of the State Board of Conservation to oversee the establishment of Iowa State Parks. However, Governor William Harding failed to appoint members to this new board until late in 1918 (Conard 1997). Pammel, who was selected to be the first chairman of the Board of Conservation, called a general meeting in 1919 to discuss priorities for the first Iowa Parks (Pammel 1919). Of the many proposals made at the meeting and included in the published report, only Ada Hayden's presentation highlighted the need for the conservation of prairies. Apparently this article was the first published recognition of the importance of creating prairie preserves, and she hoped that newly appropriated funds to the State Board of Conservation would allow this to happen. However, she would have to wait more than a quarter century for the first prairie preserves to be purchased by the state. A brief quote from this paper provides an example of Ada Hayden's beautifully descriptive writing:

Iowa is said to be a prairie state, but what is a prairie to the present generation? Within 40 or 50 years, the broad stretches of tall shining grass trembling in the sunlight or tossed by the



Fig. 1. Ada Hayden, in "College Pasture," Ames, Iowa. Date unknown. (Source: Iowa State University Department of Botany).

breezes into billowy waves, gorgeous as the season progresses with its pageant of brilliant hued flowers . . . is fast passing. . . . Few but the farm boy and the meadow lark know where the swamp now lingers, where the marigolds glitter in the marsh, where the red-brown knoll, fanned by the winds of March, turn pale lavender as the pasque flower wakes in the spring. . . . [W]hat park planting can equal a mile or two of flaming Turk's cap lily which frequents the damp native prairie in July, or the white beds of nodding anemones, the red and white sweet william, the purple patches of gauzy spiderwort, the gorgeous butterfly weed, the glowing goldenrod, and the banks of stately, radiant sunflower. All these plants are carefully cultivated by florists in parts of the country where they are not native. Why not preserve now at a small cost what cannot be replaced at any cost? (Hayden 1919d)

INTERIM WORK AND INTERESTS

Following this one-year burst of publications, her publication record about prairies largely fell silent until the 1940s. Why this 20 year hiatus? Several possible reasons are suggested by her other activities. First, she was appointed to the faculty just after getting her doctorate, so undoubtedly she was busy getting her courses established. Secondly, her friend and mentor Louis Pammel recruited her assistance on his numerous projects and publications. She wrote chapters, provided photographs and illustrations, and perhaps, along with Charlotte King, organized and edited many of these publications (e.g., Pammel and King 1926; Pammel and collaborators 1930). Pammel felt that at least those prairies that were potentially

prime agricultural land should not be permanently set aside (Conard 1997); perhaps his attitude influenced her willingness to further push for prairie preserves. Maybe, on the other hand, she had been speaking and writing about prairies, but these notes and manuscripts have not survived or been located. For example, it is unclear what role, if any, she played in drafting Iowa's 1933 25-year conservation plan (Crane and Olcott 1933). Her work on a flora of the lakes region of Clay and Palo Alto counties (Hayden 1943), claimed by Isely (1989) to have been "the best published native flora survey . . . of any part of Iowa," must have consumed a great deal of her time. Also, she probably assumed somewhat greater responsibilities in the botany department following Pammel's retirement in 1927 and death in 1931. In 1934, Ada Hayden was named both an Agriculture Experiment Station Researcher and officially the Curator of the Herbarium (Hayden papers, Iowa State University Library, Special Collections Department). She also served as an officer or on committees for a number of botanical, university-affiliated, and civic organizations (Martin 1951).

PRAIRIE PRESERVE EFFORTS RESUMED

In the final decade before her death, Ada Hayden again took up the cause of preserving Iowa's remnant native prairie areas. Louise Parker was then vice-chair of the Iowa Conservation Commission (which evolved from the State Board of Conservation) and a willing advocate for prairie preserves (Parker 1944). Ada Hayden was on the Conservation Committee of the Iowa Academy of Science and chaired the Iowa Prairie Subcommittee of the Ecological Society of America's Committee on Preservation of Natural Conditions (Martin 1951). What jump-started this interest in prairie preserves? Perhaps two factors served as the motivation: 1) a decade had passed with no action toward establishing preserves since the 25-year conservation plan had been announced (Crane and Olcott 1933); and 2) in 1941 she sold her family farm near Ames (unpubl. records, Auditor's Office, Story County) and soon saw her beloved prairie plowed for the planting of crops. Conard (1997) proposed that perhaps the "Dust Bowl" of the 1930s and publication of Sears' *Deserts on the March* (1935), both of which led to a greater public awareness of ecology, may have popularized Ada Hayden's research, thus spurring her efforts for cataloging the remaining prairie areas and pushing for their acquisition as preserves.

Isely (1989), on the other hand, speculated that she had quietly been advocating prairie preservation the entire time, but that these years were required for her evangelism to begin to bear fruit. Whatever the reason, she suddenly began to write and speak publicly with a passion and urgency of the need to get some high quality examples of different kinds of Iowa prairies set aside as preserves. The Iowa Academy of Science gave her \$100 in 1944, which was later reimbursed by the Iowa Conservation Commission (Hayden n.d., Hayden papers, Iowa State University Library, Special Collections Department), to survey and select for potential preserves the best remaining prairies across the state. She traveled to, photographed, and described 22 prairie tracts in ten counties. Her 1944 report to the Iowa Conservation Commission was published in the *Proceedings of the Iowa Academy of Science* in 1946, followed by a "progress report" in 1947 (Hayden 1946a, 1947). As early as 1944, she made an appeal to the Iowa Academy of Science recommending the purchase of these sites as prairie preserves (Hayden 1945). Of these 22 tracts, two (now Hayden and Kalsow State Preserves) were purchased for protection in her lifetime. Only three additional tracts have been set aside as preserves since 1950, although prairie habitat may yet exist on some of the remaining areas. Table 1 summarizes the current status of all 22 areas proposed by Ada Hayden as worthy of consideration for preserves.

Table 1. Status of Ada Hayden's proposed prairie preserves (Hayden 1947)^a.

County	Hayden's Site Designation	Acres Proposed (Current Size, if Applicable)	Current Status/Notes
Dickinson	No. 1 Floete Prairie	20	Cropland/Privatey owned, largely plowed in 1948 (Hayden unpubl. notes ^b); reduced to ca. 5 acres of hillside prairie above a swale
Dickinson	No. 2 Cayler Farm ^b	320(160)	Cayler Prairie State Preserve/ca. 480 acres of adjacent pasture and cropland with prairie remnants on steep slopes have recently been added, creating the Cayler Prairie Wildlife Area
Dickinson	No. 3 Higgins Estate	400	Pasture?, degraded/Privatey owned
Dickinson	No. 4 Speer Prairie	320(110)	Freda Haffner Kettlehole State Preserve
Dickinson	No. 5 Shimek Plan	ca. 1330	Prairie, pasture, crop/Little Sioux River Valley proposed by Shimek as National Preserve; includes both Cayler and Freda Haffner preserves, otherwise privately owned with some prairie remnants on rugged valley slopes
Dickinson	No. 6 Thom Farm	160(10)	Prairie, degraded/Privatey owned, voluntary protection
Emmet	No. 1 Robb Prairie	314(20+)	Largely degraded or destroyed/Possibly included at least part of Anderson Prairie State Preserve, Crimm Savanna (with small gravel prairie) and Ringham Habitat Area
Emmet	No. 2 Four-Mile Lake Prairie	10(5)	Disturbed prairie/Hayden noted presence of <i>Platanthera (Habenaria) leucophaea</i> (prob. = <i>P. praeclara</i>) and <i>Lespedeza leptostachya</i>
Pocahontas	No. 1 Kalsow Prairie	160(160)	Kalsow Prairie State Preserve
Pocahontas	No. B Gunderson Prairie	?	Cropland/Privatey owned
Howard	No. 1 Lime Springs Prairie	199(240)	Hayden Prairie State Preserve
Cherokee	No. 1 Pilot Rock Prairie	160	Pasture, degraded/Privatey owned (2 acres are "Pilot Rock Lookout")
Cherokee	No. 2 Harrison Steele Prairie	320(200)	Steele Prairie State Preserve
O'Brien ^c	No. 1 McCulla Estate (Simmons Ranch)	320	Pasture, degraded/Privatey owned
O'Brien ^c	No. 2 Steele Estate	400	Pasture, degraded/Privatey owned
O'Brien ^c	No. 3	40	Pasture, degraded/Privatey owned
O'Brien ^c	No. 4	40	Pasture, degraded/Privatey owned
O'Brien ^c	No. 5	?(21)	Prairie (at least in part)/McCormack Area (Tracy State Monument Park)
Crawford	No. 1 McWilliams Prairie	25	Plowed in the 1950's, now pasture/Adjacent to Yellow Smoke CCB Park ^d
Ida	No. 1 Hare Prairie	60	Cropland/Privatey owned, plowed fall 1948 (Hayden unpubl. notes)
Pottawattamie	No. 1 Mathews Prairie	20	Cropland?/Privatey owned
Guthrie	No. 7[1]	20	Cropland/Privatey owned

^a Table includes information provided by John Pearson (Iowa Department of Natural Resources) and from use of the Iowa State University GIS Facility, with assistance of Patrick Brown (Department of Animal Ecology/GIS Facility, Iowa State University).

^b An unpublished "working list" by Hayden from which the publication (Hayden 1947) is derived is in the Hayden papers, Iowa State University Library, Special Collections Department. This list includes site names that are not used in the publication. Also, a number of notes (such as those cited here) were added to the text in years following the publication.

^c The Iowa Department of Natural Resources' purchase of land for the Waterman Prairie Wildlife Area includes sites adjacent to or near several of those proposed by Ada Hayden. These formerly pastured areas include prairie of varying quality.

^d Information provided by Lance Nelson (Director, Crawford County Conservation Board).

Ada Hayden's concern for prairies did not stop with their "legal" protection. She and John Aikman (Hayden and Aikman 1949) proposed a guide for managing the newly acquired preserves. In this same paper, they also presented a rationale for the on-going existence of prairies in the state:

The native prairie reserve is to be regarded as an historic pre-

serve illustrative of the native cover as the settlers found it; as a living museum of fauna and flora; as a reference specimen of vegetative structure; as an example of the native landscape; and as a field laboratory where such scientific observations and experiments may be conducted as will not injure the area. (Hayden and Aikman 1949)

She took her cause for the state's acquisition of prairies to any who would listen. She wrote popular articles (e.g., Hayden 1946b), spoke to groups and clubs, and was interviewed on the radio in an effort to spread awareness of the need for prairie preservation (Hayden papers, Iowa State University Library, Special Collections Department). As alluded to earlier, she was a good photographer and artist. She hand-colored a set of lantern slides to use in her presentations (Isely 1989). She even requested that landowners consider donating their prairie holdings to the state (Hayden papers, Iowa State University Library, Special Collections Department).

Shortly after her death on 12 August 1950, the first of the prairies purchased, a 199 acre tract in Howard County, was named in her honor (Parker 1950). In 1965, a legislative act created the State Preserves Advisory Board and officially recognized state preserves as a means of permanently protecting Iowa's special sites. Today, Hayden Prairie is considered "a jewel" of the state preserves system (Leoschke and Klier 1990), and a 1995 celebration and re-dedication marked the 50th year of its acquisition.

ASSESSMENT OF HER EFFORTS AND RESULTS

As we reflect on Ada Hayden's life, what qualities did she possess that put her at the forefront of the movement to preserve prairies? Duane Isely made several statements in his tribute paper to Ada Hayden that may help us (Isely 1989). In one place, he commented about her passion for prairies, saying:

Hayden grew up with access to native prairie, fell in love with it, and was faithful to the end of her days.

In a description of her personality, he stated that:

She has been described as determined, fearless, independent, brusque and eccentric. . . . Certainly a distinctive Hayden trademark was her independence. (Isely 1989)

I'm sure these traits were of benefit to a woman willing to do field work and attempt to influence public decision in those days.

How was Ada Hayden's work viewed outside of Iowa? She was apparently quite active in the Ecological Society of America and the Ecologists' Union, along with the Grasslands Research Foundation (Billings et al. 1951; Martin 1951). In 1945 she was invited to attend the annual conference on genetics and natural history at Washington University as a consultant. This conference was led by Edgar Anderson, so at least this famous botanist must have held her in high regard. The *Ames Tribune* reported that she was extended the invitation . . .

In recognition of Dr. Hayden's contributions to knowledge of the prairie flora of the upper Mississippi Valley. (Anonymous 1945)

It is unfortunate that there are no surviving records of whether she made formal presentations of her research at national meetings or whether her contributions were primarily in committee work.

Her obituary in the *Ames Tribune* (Anonymous 1950) stated that "she was well known and respected in her field of activity throughout the country." In partial justification of this statement, the writers of her obituary in the *Bulletin of the Ecological Society of America* said,

Her name will always be associated with the exceptionally progressive conservative actions, policies, and ideas that place Iowa in a position of conservation leadership among the states. (Billings et al. 1951)

In the abstract and presentation for the Prairie Conference, I proposed that "almost single-handedly, she pioneered the idea of setting aside prairie remnants in Iowa as state preserves." In light of the

work especially of Bohumil Shimek and Ada Hayden's contemporaries in the 1940s, including Louise Parker, fellow botanist John Aikman, zoologist George Hendrickson and soils specialist Frank Riecken, is this statement really true? Dr. Isely, who personally knew her in the 1940's, seemingly agreed with my claim of Ada Hayden as THE champion of Iowa's prairies, saying:

Dr. Hayden was diversely talented and skilled. Professionally she was a knowledgeable floristic botanist and ecologist. . . . At the time I knew her [1944–1950] she was outspokenly and emotionally dedicated to the prairie effort. Commonly less than a diplomat, she was possibly most convincing to those already convinced. Consequently, her firmness of purpose, knowledge and persistence were especially effective in team effort. There, they more or less automatically rendered her a leader. (Isely 1989)

In summary, I believe Ada Hayden was uniquely qualified to be the champion of Iowa's prairie preserves. She had the scientific training to evaluate both what she saw happening in the state and the ecological literature that was coming on the scene at that time. Her academic and scientific credentials gave her an "edge" in persuading colleagues and others to join her cause. Her position as a researcher with the Iowa State College Agriculture Experiment Station provided time and support for her efforts. Finally, perhaps most importantly, her passion and vision for preserving prairies propelled her accomplishments. Her achievements may have appeared small, with only two preserves established during her lifetime; however, the legacy of her efforts furnished the framework for the current Iowa State Preserves system. Her publications remain as useful references, providing important insights into Iowa's prairies. This legacy continues to influence today's conservationists and natural historians.

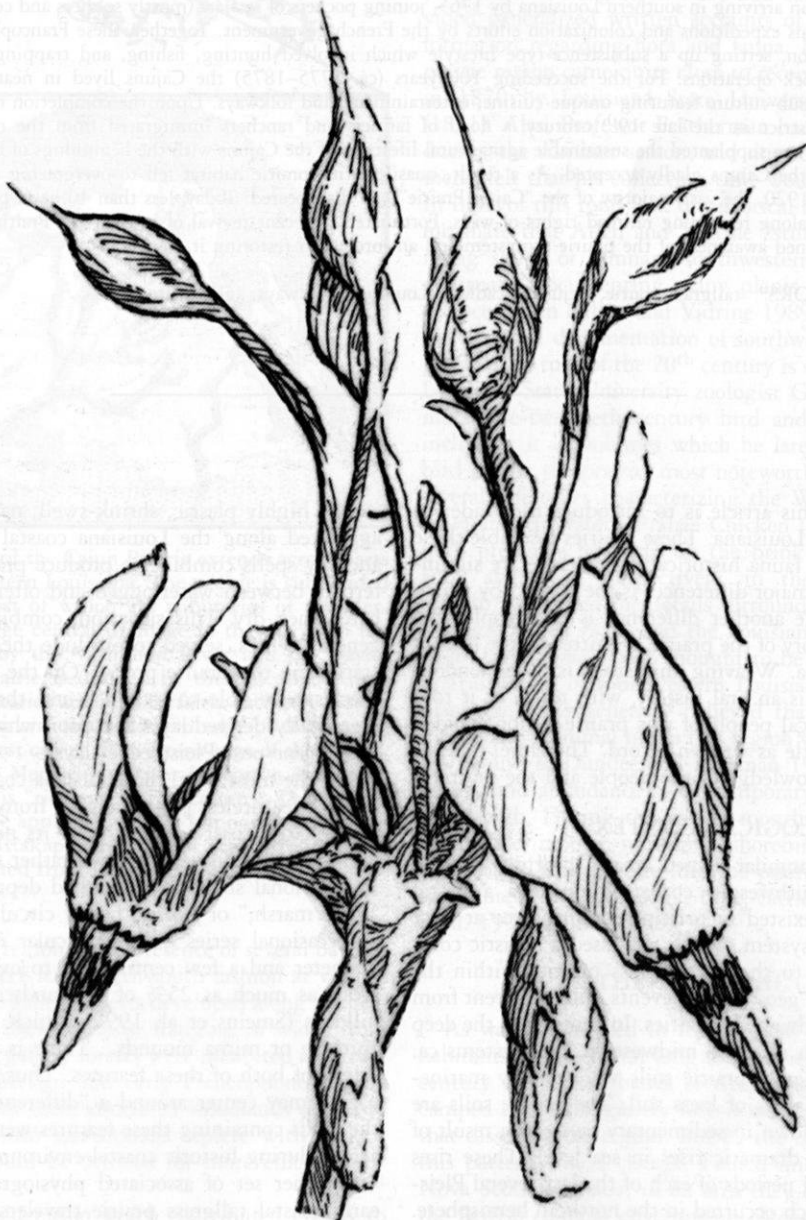
ACKNOWLEDGMENTS

I am grateful to the staff of the Special Collections Department, Iowa State University Library and the Story County (Iowa) Auditor's Office for access to their records and holdings of unpublished materials. I also thank Dorothy Baringer and Lois Tiffany, who reviewed an earlier draft and provided suggestions that improved the paper. Finally, I am grateful that Duane Isely first "introduced me" to Ada Hayden.

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Prairie Cajuns and the Cajun Prairie: A History

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Prior to the late 19th century, nearly one million contiguous ha of coastal tallgrass prairie existed in the southwestern corner of Louisiana. For the most part, the density and height of the associated vegetation precluded both the exploration and settlement of this vast habitat. French Acadians (locally known as “Cajuns”) were exiled from Nova Scotia in the mid-eighteenth century. A large number of them began arriving in southern Louisiana by 1765, joining pockets of settlers (mostly soldiers and colonial administrators) left over from previous expeditions and colonization efforts by the French government. Together, these Francophone settlers ventured into the prairie region, setting up a subsistence-type lifestyle which involved hunting, fishing, and trapping, along with limited cropping and livestock operations. For the succeeding 100 years (ca. 1775–1875) the Cajuns lived in near total isolation, thus developing a strong sub-culture featuring unique cuisine, entertainment, and folkways. Upon the completion of a railway traversing the entire prairie district in the late 19th century, a flood of farmers and ranchers immigrated from the mid-western U.S. and neighboring Texas. They supplanted the sustainable agricultural lifestyles of the Cajuns with the beginnings of high-yield agricultural technologies, which the Cajuns gladly accepted. As a result, quasi-pristine prairie habitat fell to overgrazing and the plow at ever-increasing rates. By 1920, the vast majority of the “Cajun Prairie” had disappeared. Today, less than 40 ha of prairie remains, mostly (ironically) confined along remaining railroad rights-of-ways. Fortunately, a recent revival of interest in “Prairie Cajun” folkways has resulted in a heightened awareness of the prairie ecosystem and an interest in restoring it.

INDEX DESCRIPTORS: tallgrass prairie, Cajuns, Acadians, Louisiana, folkways, agriculture.

The general purpose of this article is to introduce the reader to the prairies of southwestern Louisiana. These prairies resemble those of the Midwest in flora and fauna historically, but there are significant differences. One of the major differences is the process by which the prairie was settled while another difference is the people who settled this prairie. The history of the prairie is knitted to the history of the people and vice versa. Weaving this story is a tremendous challenge because the story is an oral history, with much of it told in several languages. The local people of this prairie region avoided education and, thus, left little as written record. Therefore, the following portrays our best knowledge of the people and the prairie.

THE ECOLOGICAL CONTEXT

Once encompassing a triangular-shaped area of nearly 1 million contiguous ha within the southwestern corner of Louisiana, a coastal tallgrass prairie ecosystem existed in pristine condition for at least 12,000 yrs. Curiously, this system, which possessed a floristic community remarkably similar to that of tallgrass prairies within the midwestern U.S., arose from geo-climatic events quite different from that of the better known midwestern prairies. In contrast to the deep layers of loessial soils blown into the midwestern U.S. systems ca. 12,000 yrs ago, coastal tallgrass prairie soils were mostly marine-derived with only shallow layers of loess soil. The prairie soils are tight, calcareous clays laid down in sedimentary layers as a result of coastal flooding due to the dramatic rises in sea level. These rises characterized the interglacial periods of each of the last several Pleistocene “Ice Age” events which occurred in the northern hemisphere.

The highly plastic, shrink-swell, nature of clay soils is much exaggerated along the Louisiana coastal zone, where alternating wet and dry spells combine to produce prairie soil conditions which alternate between waterlogged and often anoxic when wet and rock-hard when dry. This situation, combined with frequent lightning-generated fires, served to preclude the establishment of woody vegetation on the prairie proper. On the other hand, herbaceous plant species were able to establish and thrive upon the relatively thin, organically-derived layer of topsoil which gradually formed above the Pleistocene/post-Pleistocene clays.

For the most part, the Louisiana coastal tallgrass prairie region is a rather featureless plain, ranging from ca. 1.5 m in elevation nearest to the Gulf Coast to ca. 16 m at its northern reaches. However, the region is characterized by two rather subtle physiographic features: 1) occasional shallow water-filled depressions, referred to as *marais*, “little marsh,” or *platins*, nearly circular ponds, by the Cajuns, and 2) occasional series of low, circular mounds, ranging 2–20 m in diameter and a few centimeters to over 1.5 m in height. In some areas, as much as 25% of the landscape may be covered by these hillocks (Smeins et al. 1992), which are most often referred to as “pimple or mima mounds.” There is ongoing conjecture as to the origin of both of these features. Thus far, the most plausible explanation may center around a “differential erosion” concept whereby the lands containing these features were subjected to wind and wave action during historic coastal environments (Smeins et al. 1992).

Another set of associated physiographic features which allowed early coastal tallgrass prairie travelers to more easily navigate and

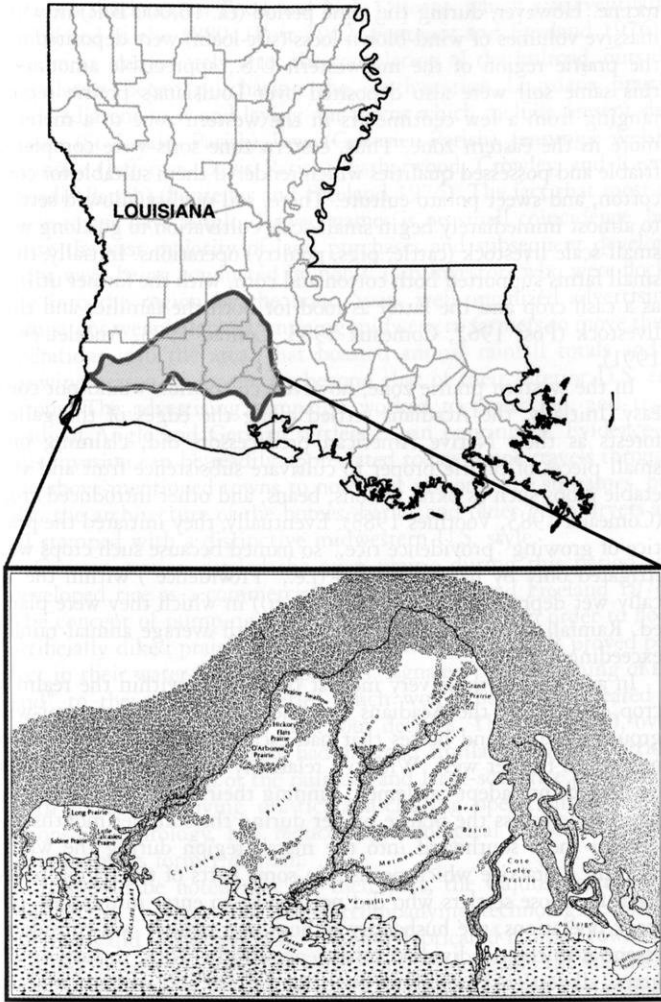


Fig. 1. The historical range of the Cajun Prairie extends across parts of eight parishes in southwestern Louisiana. The prairie is subdivided by a number of streams, most of which are tributaries of the Mermentau River system (the large central drainage in the map). To the east, the prairie is drained by the Vermilion River and the Bayou Teche, while the western prairie is drained by the Calcasieu River. These streams and their tributaries are lined by fairly extensive gallery forests. Lafayette is the largest city at the eastern edge of the prairie, while Lake Charles is the largest city at the western edge of the prairie. Much of the area east of the Mermentau River is "cotton and corn" country, while the area west is "rice and cattle" country. The earliest settlements of the Cajuns were approximately 20 km north (Opelousas frontier) and 10 km south (Attakapas frontier) of the current city of Lafayette. The maps are adapted from Newton's (1972) atlas.

orient themselves within the region is the presence of several bayous, sluggish streams, which dissect it in north-south fashion at various intervals. Riparian hardwood, gallery forests developed along the better-drained natural levees of these streams. Ranging in width from 10–1000 m, these strip-like, gallery forests were inhabited and traveled through by Native American and early Francophone settlers alike. Also, these streams with their associated woodlands served to separate the vast grassland into sub-sections replete with various wooded landmarks which could be utilized for more efficient orienting (Fig. 1).

A final physiographic consideration which contributed greatly to

the eventual cultural disposition of southwestern Louisiana's prairie region involves its degree of physical isolation resulting from the ecology/physiography of the lands which surrounded the region. To the north, the prairie system was bounded by a substantial pine/hardwood "flatwoods" system possessing sandy soils, that were too nutritionally poor and/or wet to clear for crops. Together with eastern Texas, much of that area was considered the Big Thicket (Ajilvsgi 1979). To the east lay the vast Atchafalaya Basin, one of North America's largest river swamps, and the entire southern edge of the prairies was bounded by an equally impenetrable mosaic of freshwater, brackish, and salt marshes.

The prairie region was isolated from the East by the immense Atchafalaya Basin, but the Attakapas people, a primitive and nomadic Native American group, occupied it. Few non-native people settled or even surveyed the region prior to the mid to late 18th century (Kniffen 1965). Finally, during the 19th century, land surveyors C. C. Robin (1807) and Samuel Lockett (1969) visited small portions of the region in 1803 and ca. 1850, respectively, and provided generalized written accounts of it, containing very little information regarding flora and fauna. Before it was obliterated, the prairie region came quite close to receiving a proper botanical survey in 1870 by Louisiana State University botanist, A. Featherman (1871). Alas, Professor Featherman had arrived at the prairie region during the summer season, and due to the lack of blooming specimens, felt that his collecting time would be better served elsewhere. In light of this total lack of historical botanical documentation, it is fortunate that Allen and Vidrine "stumbled" onto the last few existing strips of remnant southwestern Louisiana prairie in 1986, eventually documenting many plants and animals associated with the ecosystem (Allen and Vidrine 1989 and 1990).

Historical documentation of southwestern Louisiana prairie fauna prior to the turn of the 20th century is similarly lacking. Fortunately, Louisiana State University zoologist George Lowery, Jr. amassed as much pre-twentieth century bird and mammal data as he could, including it in volumes which he later authored. Of the historical bird life on the prairie, most noteworthy from Lowery (1974a) were several references characterizing the Whooping Crane (*Grus americana*) and Attwater's Prairie Chicken (*Tympanuchus cupido attwateri*), both presently hovering on the brink of extinction, as "common" and "abundant," respectively, in the region. Similarly, Lowery (1974b) recounted the details surrounding the discovery of both the red wolf (*Canis rufus*) and the Louisiana prairie vole (*Microtus ochrogaster ludovicianus*), both thought to be presently extinct, within the prairie region of southwestern Louisiana. Like that of the region's plant life, it is generally believed that historical bird, amphibian, reptile and mammal life in this region was extremely diverse (Lowery 1974a and b, Dundee and Rossman 1989, Johnson 1999). The diversity and abundance of contemporary mammal life were substantially high. During the winter months in particular, notably large numbers of raptors, waterfowl, shorebirds, sparrows, blackbirds, and other birds still migrate into the prairie region, now almost totally supplanted with rice, sugar cane, cattle, and crayfish farms (Vidrine et al. 1995, Huner 2000).

THE CULTURAL CONTEXT

As was emphasized in the previous section, the only human inhabitants of the coastal tallgrass prairie region prior to the mid 18th century were small bands of Attakapas Indians, who seasonally encamped along the gallery forests associated with the various bayous that dissected the region. But by the latter half of the 18th century, this pattern would change. French immigrants who had settled in Nova Scotia, Canada, in an area they called *Acadie*, were exiled by the British colonial government, ostensibly on the basis of religious

differences, in 1755. Some of these exiles went back to France, but most of them spent the next decade wandering the Atlantic coast in search of colonies that might take them in. While some were eventually accepted into various New England colonies, most were not. Eventually, the "Acadians" got word of French colonies that existed along the north-central coast of the Gulf of Mexico and began making their way to this region. Between 1764 and 1788, an estimated 2635 Acadians arrived in the Louisiana colony followed in 1809 by a still-unknown number. These were quickly relocated west of the Mississippi River along the eastern edge of the prairie region (Brasseaux 1987 and 1991). During this period, French and/or Spanish settlement in that region was scanty and limited to clusters around two military installations: the *Poste des Attakapas* in present-day St. Martin Parish and the *Poste des Opelousas* in present-day St. Landry Parish. Upon arriving at these areas, the Acadian exiles, who already possessed a long tradition of subsistence farming, livestocking, hunting, fishing, trapping, and gathering, wasted no time in removing themselves from these established settlements. Some moved east into the great Atchafalaya Swamp, and others moved west into the prairie. Prior to this time period, some non-Acadian French settlers, mostly retired soldiers from previous expeditionary and occupation forces, along with a few Spanish settlers were established along the edges of the prairie. The prairie area remained under Spanish governance through the end of the 18th century; however, first the French gained control and then sold the area to the Americans at the beginning of the 19th century. Against the background of governmental change, the settlers were already employed in small-scale farming and ranching activities along the northern and eastern boundaries of the prairie region (Comeaux 1983).

The migration of these French settlers was heralded in the epic poem *Evangeline* by Longfellow (1847). Other non-Cajun myths and stories developed on the prairie and its associated environs. Two of the most famous characters were Jean Lafitte, the pirate, and Jim Bowie, knife-fighter and speculator; interestingly these two were contemporaries in both business and adventures in the surviving stories (Ramsay 1996, Thorp 1991). However, it is the Prairie Cajuns that have received the greatest attention. The Jean Lafitte National Historic Parks of Louisiana commissioned a detailed study of the Cajuns and produced a five-volume project report (in Ancelet et al. 1991). The park system houses it in the Prairie Cajun visitor center in Eunice, Louisiana.

Over time, the Cajuns gradually became entrenched within the prairie proper, doubtlessly finding the long growing season (compared with that of France and Canada), plentiful game, and seemingly infinite range of livestock forage well-suited for their subsistence lifestyles. But living there was by no means easy, due primarily to the great difficulty experienced in carving out a homestead and/or traveling for even short distances amidst exceedingly thick and tall prairie vegetation (Fontenot and Freeland 1976). Lifelong Evangeline Parish (north-central boundary of the prairie) resident Burkeman Veillon (born: 1921) once recounted to one of the authors stories from his grandfather (ca. 1870–1890) of men traveling on horseback through the "Mamou Prairie" where the only things visible of them were their hats!

Living there in near-total physical and cultural isolation from the rest of colonial America, a strong, resilient, and ultimately fascinating culture would develop over the next 100 yrs.

Agriculturally, the prairie could be divided into two cultural zones, the "corn and cotton" zone in the east and a larger "rice and cattle" zone in the west (Comeaux 1983). The reasoning for such a division lies in the soils and the lay of the land. As previously mentioned, the bulk of southwestern Louisiana prairie soils are dense calcareous clays derived from repeated flooding/sediment laying via the adjacent Gulf of Mexico during interglacial periods of the Pleis-

tocene. However, during the same period (ca. 10,000 B.P.) in which massive volumes of wind-blown loess (silt-loam) were deposited over the prairie region of the midwestern U.S., appreciable amounts of this same soil were also deposited over Louisiana's prairie region, ranging from a few centimeters in the western zone to a meter or more in the eastern zone. Thus, eastern zone soils were completely friable and possessed qualities which rendered them suitable for corn, cotton, and sweet potato culture. There, soil quality allowed settlers to almost immediately begin small-scale cultivation to go along with small-scale livestock (cattle, pigs, poultry) operations. Initially, these small farms supported both cotton and corn, with the former utilized as a cash crop and the latter as food for both the families and their livestock (Post 1962, Comeaux 1983, Conrad 1983, Ancelet et al. 1991).

In the western prairie zone, however, cultivation would not come easy. Initially, the Acadians settled along the edges of the gallery forests as their Native American predecessors did, claiming only small pieces of prairie proper to cultivate subsistence fruit and vegetable crops such as okra, melons, beans, and other introduced crops (Comeaux 1983, Voorhies 1983). Eventually, they initiated the practice of growing "providence rice," so named because such crops were irrigated only by natural rainfall (i.e., "Providence") within the locally wet depressions (*marais* and *plattins*) in which they were planted. Rainfall is generous in the region, with average annual rainfall exceeding 1.25 m.

In addition to these very modest beginnings within the realm of crop cultivation, the Acadians also encountered remnant semi-wild groups of cattle and horses that had escaped from Spanish colonial operations further west. Within a relatively short time the Acadians developed into adept cattlemen, running their herds "free range" (*au large*) style across the prairie proper during the summer months and driving them southward into the marsh region during the winter months, a practice which persists in some parts of the region today. Even for those settlers who did not choose to enter into larger livestock operations, the husbandry of hogs and poultry was considered essential to their individual subsistence efforts. Thus, to varying degrees, all settlers throughout both the eastern and western zones of the prairie region necessarily entered into both crop cultivation and livestock operations in a dual system that is still employed by the majority of contemporary prairie region inhabitants.

The Cajun culture remains complex with distinctive folkways (e.g., cuisine, language, medicine, music, and religious traditions). These are discussed in several sources (Lynch 1942, Newton 1972, Dormon 1983, Savoy 1984, Holmes 1990, Ancelet et al. 1991, Fontenot 1992, Reese 1992, Vidrine et al. 1995).

THE DEMISE

By 1850, New Orleans was already a 130-year-old city, and its ever-increasing population was already outstripping the steady supply of agricultural products which flowed into it from surrounding rural areas. The supply of beef in particular was most problematic because lands suitable for cattle ranching were in short supply to the north and east. At that time, any goods shipped into New Orleans from the west faced a treacherous boat journey across a 60–70 km maze of shallow lakes, swamps, rivers, and bayous within the Mississippi River floodplain and the great Atchafalaya Swamp to its immediate west (Davis 1968). Barguing live cattle across this massive swamp complex with its ever-fluctuating water levels was out of the question; and because a boat trip across that forested wetland system could take 3–6 weeks (depending on water levels), shipping processed meat was logistically impossible as well. Thus, the only viable option which remained was the construction of a railway system

between southeastern Texas and New Orleans, which was eventually completed in the 1880s (Post 1962, Fontenot and Freeland 1976).

Almost immediately after the completion of the railroad, outside speculators began purchasing the southwestern Louisiana prairie lands adjacent to it and laying out towns which include present-day Eunice (St. Landry Parish), Iowa (Calcasieu Parish), Jennings, Welsh, Roanoke (Jefferson Davis Parish), Estherwood, Crowley, and Rayne (Acadia Parish) (Fontenot and Freeland 1976). The fact that most of these towns have Anglo-derived names is no small coincidence, because the vast majority of land purchases and subsequent development were being conducted by non-Cajun investors who were flocking into the region by the hour. Soon, well-organized advertising campaigns were launched, enticing midwestern farmers to move their operations into the area, that boasted annual rainfall totals and a growing season that were far beyond that of their interior U.S. environs. The advertising campaign worked to perfection, and train loads of Anglo and German settlers began pouring in. Evidence of this invasion can be readily appreciated today as one travels through the above-mentioned towns to note that not only the surnames, but also the architecture of the homes, barns, and older grain dryers are all stamped with a distinctive midwestern U.S. style.

German settlers settled the open prairie during this period and developed rice as a commercial crop (Fontenot and Freeland 1976). The concept of pumping water out of local bayous in order to flood artificially diked prairie lands, whose dense clay subsoils proved perfect in their water-holding capacities, signaled "the beginning of the end" to the ecological prairie, which would be hastily cleared in wholesale fashion over the next four decades. Thus, by 1920, overgrazing (the cattle industry had attained similarly epic proportions upon the completion of the railroad) and large-scale rice production, with its accompanying drastic land-clearing operations and alterations in hydrology, had reduced the ecological prairie to a mere fraction of its former domain.

It should be noted that for their part, the Cajuns heartily embraced the Germans and their accompanying technologies, for the Germans did not linger within the pre-fabricated railroad towns but instead dived right into the prairie proper alongside the Cajuns. In fact, within the space of only one or two generations, the majority of German settlers had become virtually indistinguishable from their Cajun brethren. Like the Spanish prairie settlers before them, the Germans were overpoweringly and rapidly absorbed into the Cajun lifestyle in an ongoing cultural phenomenon which remains in force today. It is obvious that southwestern Louisiana prairie dwellers of Spanish, German, African, and even Native American extractions all contributed shares of folkways that entered the mix of what is known today as "prairie Cajun culture." However, it is equally apparent that the overwhelming majority of descendants of these various ethnic contributors have taken on the foods, customs, religious customs, music, and language of the Cajuns. In part, the underpinnings of this phenomenon can be explained by the simple fact that Cajun women substantially outnumbered the women who would arrive later with the non-Cajun settler groups, and, as a result, a greater number of non-Cajun men would necessarily marry into Cajun families. As is usually the case with most ethnically mixed marriages, the children are more apt to take on the customs, beliefs, etc. of the mother (Ancelet et al. 1991, Brasseaux 1991, Brasseaux et al. 1994).

In efforts to mainstream Cajun children into American culture, the Cajun French language was forbidden to be spoken on school property by the mid-1920s. Further mainstreaming events would occur in relatively rapid succession with the advent of the automobile, World War II (where the majority of young Cajun men would discover and absorb American culture firsthand), the television, and other technologies. Therefore, by 1950 the prairie Cajun culture would exist as a mere shadow of its former self, and the Cajun Prairie

would be reduced to fragments so small as to be completely forgotten by its inhabitants.

Fortunately, this period of cultural demise would end almost as suddenly as it began, with the establishment of the Council for the Development of French in Louisiana (CODOFIL) in 1960. Initially comprised of a small group of Cajun musicians, educators, and politicians, membership and interest in this organization mushroomed over the next 20 yrs. As a result, Cajun heritage programs, conferences, and facilities began to spring up throughout the region, and the Cajun French language found its way back into the school system.

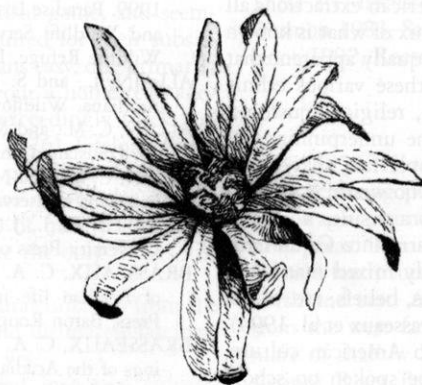
By 1984 interest in both the cultural and ecological aspects of the Cajun Prairie ignited within the staff of the Lafayette Natural History Museum in Lafayette, Louisiana and culminated in the opening of a Cajun Prairie exhibit at that facility in the fall of 1986. In that same year, Louisiana State University at Eunice biologists would rediscover remnant strips of Cajun Prairie along the right-of-ways of the same railroads which had initiated its demise some 100 yrs earlier.

The latest chapter in the story of the Prairie Cajuns and the Cajun Prairie involves the initiation of several ecological restoration projects (Allen and Vidrine 1989 and 1990, Fontenot 1992, Allain and Johnson 1997, Allain et al. 1999). Sadly, because no adequate pre-settlement vegetational records exist for the region, the present restoration efforts represent collections of those residual plant species that have persisted within the small remnant strips. By the same token, it has already become evident that these residual plant species are creating a vegetational matrix which appears to exclude the majority of invasive exotic plant species present within the region and attracts and supports a surprisingly high diversity of native animals, both vertebrate and invertebrate. Workers are thus hopeful that over time, the entire community of organisms that once constituted the historical coastal tallgrass prairie may recreate a habitat that closely approximates that of the original (Vidrine et al. 1995, Vidrine and Borsari 1998). Hopefully, this will inspire its human inhabitants to more ethically understand the complete circle of life where the land itself comes to be viewed as the real community to which the people belong (Leopold, 1949 and 1999, Jackson 1999).

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Discovering the Prairie in Your Own Backyard: A Workshop Introducing Northern Loess Hills Prairies to Elementary Teachers and Their Students

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In early September 1997, 13 teachers from nine different schools in the Sioux City region attended *Discovering the Prairie in Your Own Backyard*, a day-long workshop designed to encourage elementary teachers to incorporate prairie-related materials into their lesson plans by giving them confidence to lead their own students on a field trip to a local prairie. The workshop, funded by the Andrea and Norman Waitt, Jr. Foundation and directed by the senior author, included a multi-media introduction (35mm slides, video clips, and relevant Internet web sites), field trips to local prairies, a stop at the Dorothy Pecaut Nature Center, and demonstrations on plant specimen collecting, pressing, and mounting. Throughout the remainder of September and part of October, participating teachers returned to the field with their students for first-hand prairie experiences. At least 250 area students from kindergarten to sixth grade were initially exposed to prairies on these field trips. Students from one school, Everett Accelerated Elementary, have enthusiastically continued their fascination with prairies as a result of this workshop.

INDEX DESCRIPTORS: Loess Hills, Prairie Education.

The Loess Hills of western Iowa are a unique landform of steep hills forming a narrow (1–5 km; 3–10 mile) band extending for about 320 km along the east side of the Big Sioux and Missouri river floodplains. The Loess Hills are composed of glacially-derived silt first transported here by meltwater 12,000–31,000 years ago. Next, prevailing westerly winds transported exposed silt eastward, especially in the winter months when river levels were lower, periodically redepositing it in thick drifts adjacent to the floodplain. Over the last 12,000 years, weathering by rain has shaped these drifts into the hills of today (Mutel 1989).

Prairies are perhaps the most celebrated natural community in the Loess Hills. These prairies tend to host species assemblages more typical of the Great Plains compared to the rest of Iowa due to porosity of the soil, intense sunlight, and strong winds (Mutel 1989). The relatively rugged topography of these hills has frequently discouraged cultivation, permitting the persistence of large prairie remnants. Such prairie remnants even occur within the city limits of Sioux City (pop. 80,000), the principal metropolitan area in the northern Loess Hills. The largest of these remnants, the 61 ha (150 acre) Sioux City Prairie, is owned and managed by The Nature Conservancy (TNC) and lies just to the west of Crescent Park, one of the city's northern neighborhoods.

This proximity of high quality prairie remnants affords a prime opportunity for area students to become personally acquainted with prairies, yet few opportunities exist for their teachers to become familiar with prairies as an educational resource. *Discovering the Prairie in Your Own Backyard* was designed to enable elementary teachers to incorporate prairie-related materials into their lessons by giving them confidence to lead their students on a prairie field trip. The workshop's basic assertion was that area elementary teachers and their students would develop a greater understanding and respect for prairie ecosystems through field studies of the Loess Hills and its native prairies. The workshop targeted elementary teachers because of the impressionable age of their students.

Briar Cliff College, with its campus adjacent to the Sioux City Prairie's northeast corner, served as the ideal host for the workshop, which was funded by a grant from the Andrea and Norman Waitt, Jr. Foundation, now the Kind World Foundation. In April, 1997, all elementary schools within a 30-min. drive of Briar Cliff College received announcements and applications for the workshop. The workshop would accept up to 20 teachers, and a field trip fund was established to assist participating teachers to take their students to a local prairie.

THE WORKSHOP

On 6 September 1997, 13 teachers from nine schools participated in the workshop. The senior author directed the workshop assisted by three Briar Cliff biology majors and one member of the Loess Hills Audubon Society. Participants were provided with an information packet which included background on the Loess Hills, maps of local prairies, a checklist of easily found plant species, a compilation of video and book resources, and a list of prairie-related Internet sites. Participants were introduced to prairies with 35mm slides, clips from prairie-centered films, and an Internet demonstration focusing on prairie-related sites.

After the introductory talk, the group spent the remainder of the morning exploring the northern portion of the Sioux City Prairie. This session centered on the geologic formation of the Loess Hills and introductory identification of fall-blooming prairie plants. Near the conclusion of this outdoor session, a short demonstration was given on plant collecting and pressing. Teachers who so desired were encouraged to collect above-ground specimens on Briar Cliff property to avoid collecting on a TNC preserve.

In the afternoon, the group focused briefly on plant pressing and preparing labels for their recently collected specimens. They also mounted specimens (complete with labels) of big bluestem (*Andropogon gerardii*) which had been collected two weeks earlier in anticipation of the workshop. This component of the workshop provided

the elementary teachers with a "make-and-take" opportunity that could be applied later in their classrooms.

The majority of the afternoon was spent on a short hike at Broken Kettle Grasslands, a 850 ha (2,100 acre) TNC preserve about 24 km (15 miles) north in Plymouth Co. This activity allowed the participating teachers to experience another prairie and to easily observe the contrast between the Loess Hills and the adjacent flood plains of the Missouri and Big Sioux rivers. Broken Kettle Grasslands also provided additional opportunities to apply plant identification skills first learned at the Sioux City Prairie that morning. On the trip back to Briar Cliff, the group made a brief stop at the Dorothy Pecaut Nature Center to review its prairie exhibits and to examine the Center's nature library.

At the end of the day, participating teachers were surveyed as to which of the activities stood out. In response, the majority noted the prairie hikes and the opportunity to experience the prairie environment first-hand. Comments such as "hands-on learning is so much more effective" and "being in the prairie, feeling the atmosphere, seeing and touching the different kinds of plants and naming them" characterized the interactive learning of the workshop. One participant stated she "was actively engaged in my own learning" while another declared "seeing actual plants is far superior than looking at pictures." Some also stated it was "amazing to think this is right in Sioux City" and the workshop helped them "to understand first hand what we've been teaching."

The workshop met the teachers' expectations, and many explicitly stated that they would be able to incorporate prairie subjects in their lesson plans. Among the written comments were also expressions of appreciation and declarations of feeling "more secure . . . so that the children will feel more comfortable and knowledgeable" and feeling "a little more comfortable discussing the 'prairie' after having experienced it first-hand."

PRAIRIE EDUCATION AFTER THE WORKSHOP

During the rest of September and part of October, the participating teachers led their students on prairie field trips. At least 250 area students from kindergarten to sixth grade were initially exposed to prairies on these field trips, which were usually made to the Sioux City Prairie. Depending on their schedules, the biology majors who assisted during the workshop sometimes served as facilitators on these trips. These field trips were subsidized by a field trip expense fund, about \$150/teacher, which was provided through the workshop's grant. This fund covered field trip expenses such as bus rental, drivers, and gas. If the teachers' schools covered the field trips, then the money allocated to each teacher could be spent instead on prairie-related teaching resources such as films, videos, books, and posters.

Although the prairie field trips were a central experience for all, field instruction and subsequent classroom activities were at the discretion of each teacher. As an example, teacher Sheryl Banks, assisted by interested parents, combined both her morning and afternoon kindergarten classes from Harney Elementary School in South Sioux City to make an all-day field trip to Stone State Park. After studying the displays in the Dorothy Pecaut Nature Center, they hiked a short distance through woods to reach a ridge-top prairie.

Based upon the responses of her students in the classroom, Ms. Banks soon discovered that this fall experience provided her students with a good foundation for learning throughout the rest of the school year. By visiting the Nature Center and the nearby prairie, Ms. Banks believed that her students better understood the interrelationships existing among living things and the importance of conserving natural resources than they would have by learning about prairies only through class presentations. A prairie enthusiast herself, Ms. Banks was thrilled to learn that her students' interest in prairies was shared

among their families. Some families even began to visit prairies and other habitats in Stone State Park on their own.

Post-workshop interviews with the participating teachers revealed that science and ecology were among the most frequently enhanced subjects as a result of this workshop. Kris Flewelling at McKinley Elementary thoroughly integrated prairie studies into her fourth-grade science curriculum. Meanwhile, Delores Ward regularly incorporated examples from their prairie field trip when her fourth-graders at Riverview Elementary studied plants, insects and spiders, and the environment. Her class's enthusiasm for prairie studies even spread to others within the school. In Jackson, Nebraska, Gary Ham's fifth- and sixth-grade classes also became very interested in their prairie studies. After visits to both the Sioux City Prairie and the Dorothy Pecaut Nature Center, his students engaged in hands-on classroom activities that included both identifying and mounting plants and drawing prairie landscape scenes. They immersed themselves in learning about the Loess Hills and the prairie, and in Mr. Ham's words, "became fully aware of the prairie and its importance in our world."

Not only did students gain a greater understanding and respect for prairies, some participating teachers also found ways to infuse prairie topics into mathematics, writing, and social studies. For example, Margaret Swanson at Bryant Elementary integrated her fifth-graders' prairie learning into several already existing units such as those on Lewis and Clark and regional history.

Perhaps the best measure of the success of *Discovering the Prairie in Your Own Backyard* came from Everett Accelerated Elementary School (EAES). Its students' on-site prairie activities on the Sioux City Prairie incorporated a variety of experiences. Students gained a sense of what a prairie was during a walk filled with touching, seeing, and smelling of the grasses and wildflowers. Many students were asked to draw and/or explain what they observed about the flora and the fauna of the prairie ecosystem. Words describing the prairie were jotted down for later use. Because the field trips occurred in the fall, students focused on different kinds of seeds. They also compared the prairie to the surrounding human-influenced environments. Some drew landscape pictures in the field while others used calculation, estimation, and measurement skills to discover other aspects of the prairie.

The teaching team of fourth- and fifth-grade teachers from EAES (Cyle Murray, Joanne Gibson, LeaAnn Jefferson, Dan Burrows, and Jo Yaeger) subsequently created a prairie-centered thematic unit impacting all areas of the curriculum. This unit included both nonfiction and fiction books read to and by the children, student-composed poetry and narrative writings, and the history of the Loess Hills and its native prairie. In addition to topics in prairie ecology, problem-solving situations involving the prairie were posed to the students. Drawings, collages, dioramas, and other illustrations were encouraged. A prairie garden was even planted and maintained by students and staff. Prairie studies have continued at EAES since the team's initial exposure to prairies during the workshop.

Among the unanticipated outcomes from this workshop was the rapport which developed between the senior author and EAES. This school showed substantial interest in the workshop by sending five of its teachers. In response to this enthusiasm, Dr. Hazlett assisted with Everett's September field trip to the Sioux City Prairie and later accepted an invitation to speak before an assembly at the school in late January 1998. Students followed up on these visits by sending him e-mail messages that included comments on their recent studies.

EAES students maintained their fascination with prairies through continued field visits to the Sioux City Prairie. In October 1998 and 1999, students, with the help of Iowa TNC staff, collected seeds of prairie plants from the adjacent Sioux City Prairie to assist in the restoration of a hillside on Briar Cliff College property which had

been badly damaged during a construction project. During a trip in May 1999, the students returned to scatter these seeds over the damaged area. Much to the delight of the EAES students, Dr. Hazlett joined each of these field trips.

SUMMARY

Discovering the Prairie in Your Own Backyard achieved its goals. It provided the confidence, skills, and resources for participating elementary teachers to lead their students on a Loess Hills prairie field trip and thereby permitted the active incorporation of prairie subjects into their lesson plans. Local teachers have grown in their interest in prairies. Their students have become enchanted with our regional prairies due to their first-hand experiences and subsequent classroom instruction.

ACKNOWLEDGMENTS

First, we'd like to thank Sunday Ford, Heidi Jacobson, and Katie Peterson, the Briar Cliff biology majors who assisted in the workshop and, when schedules allowed, helped the teachers who returned to the Sioux City Prairie with their students. We are grateful to Bob Moritz (now known as Audubon Bob to scores of Everett students) for lending his expertise with birds during the workshop as well as sharing his love for nature on subsequent Everett prairie field trips. We especially thank the Kind World Foundation for funding *Discovering the Prairie in Your Own Backyard*.

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Electronic Guide to Wildflowers: Maintaining an Online Database for Natural Areas

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An online guide to wildflowers of the Saylorville Lake Recreation Area, Des Moines River Basin, Polk Co., Iowa, is maintained as a public information project in cooperation with the U. S. Army Corps of Engineers. Each wildflower is represented by a digital image and scientific description. Digitally created diagrams of leaf and flower structure are also included. Issues associated with maintenance of the online guide are discussed. These include: (a) collection of data and online delivery methods, (b) features of a traditional guide compared to those of an electronic guide delivered online, (c) an electronic guide as a database, (d) incorporating online data in CD-ROM and PDF formats, and (e) publishing online data through the peer review process.

INDEX DESCRIPTORS: electronic publishing, Iowa wildflowers, electronic wildflower guide, flower databases, online wildflower guide, website publishing.

An online visual-guide to the wildflowers of the Saylorville Lake Recreation Area, Des Moines River Basin, Polk Co., Iowa, is maintained as a public information project in cooperation with the U. S. Army Corps of Engineers, Rock Island District, Illinois (Wacha 2001a). The principal goals of this web-based guide are (1) to maintain an online database that features descriptions of local wildflowers as an informational resource for use by the public, and (2) to produce a CD-ROM of this resource which will be available to the public at the Saylorville Lake Visitor Center through a kiosk operated by the Iowa Academy of Science. The CD-ROM (Wacha 2001b) provides information similar to that presented in the online guide and contains a Portable Document File (PDF) from which printed copies of the guide can be generated for use in the field.

In this paper we discuss issues that may be useful in developing and managing a website directed toward public awareness of native and restored natural areas. The paper is divided into four sections. The first provides background information describing: (a) the Saylorville area, (b) the rationale for serving the guide on the World Wide Web, and (c) the methods used in collecting the data and placing it online. The second section compares the differences between a traditional field guide and an electronic guide as a means of understanding the limitations and advantages of their competing formats. Section three examines the management of online databases (or websites) with particular reference to the Saylorville website. The final section discusses online databases as publications. We hope these discussions will provide some insight into the theory and operation of a web-oriented database and, perhaps, inspire the development of other online sites as public links to our natural areas.

BACKGROUND

The Online Guide

The online guide presently contains 45 taxa, including prairie and woodland species, within the families Asteraceae, Ranunculaceae, and Rosaceae. The guide is being expanded to include additional species in other families. Each taxon in the guide is represented by a digital image and a scientific description based on specimens found and collected at the Saylorville site (Fig. 1). Family descriptions, a glos-

sary, and digitally-created diagrams of leaf arrangement and flower structure (Fig. 2) are also included. Taxa presented in the website are grouped by family. Within families, species are grouped by flower color and arranged alphabetically by common name.

The Saylorville Area

The Saylorville Lake Project in Polk Co., Iowa (Fig. 3) is administered by the U. S. Army Corps of Engineers. It hosts many visitors and has numerous recreational facilities for water sports, camping, picnicking, hiking, and bicycling. Still, much of the Saylorville Project remains an undeveloped non-recreational area. Two major vegetation zones are associated with the area: (1) bottom-land forest which lies along the Ding Darling Greenway (Des Moines River corridor) south of Saylorville Lake and below Saylorville Dam, and (2) upland forest, which borders Saylorville Lake above the Dam, north to Big Creek Lake. These wooded landscapes are periodically interrupted by ponds, oxbows, streams, fields, savannas, parcels of planted and native prairie, and the park-like camping and picnic sites within the 10,500 ha Saylorville Project. These diverse habitats provide the area with a variety of wildflowers throughout the growing season. A multipurpose, bicycle-hiking trail extends along the entire east side of the Ding Darling Greenway, Saylorville Lake, and Big Creek Lake. A journey along this trail provides access to those habitats in which the wildflowers presented in this guide have been observed.

Rationale for an Electronic Guide

The U. S. Army Corps of Engineers at Saylorville Lake strives to promote stewardship of its natural resources for its visitors. Increased knowledge among resource users not only leads to increased enjoyment but also can influence environmental attitudes and behavior (Gigliotti 1990). If visitors and adjacent landowners of Saylorville Lake become more knowledgeable about the wildflowers around them, they may develop an even greater interest in the area. Promoting educational media is an effective way of improving knowledge and favorable attitudes among recreational users and neighboring citizens (Marynowski and Jacobson 1999). A fundamental reason

**A Guide to Common Wildflowers of the Aster Family in the Saylorville Lake Area
of Central Iowa**

Compass Plant
Silphium laciniatum



Flowering heads have from 15 to 30 yellow ray flowers surrounding a central cluster of yellow disc flowers. Involucral bracts are hairy, large, and broadly ovate, with pronounced recurved-tips that taper to a long, narrow point. Flowering heads are distributed sparsely along the upper stem, which has a "zig-zag" appearance. Upper stem may bear clear drops of resin. Leaves are highly lobed, almost to the point of being compound, and are larger and more densely clustered at the base of the stem. Leaves attach individually by a petiole that bears small wings. Leaf edges may be aligned in a north-south direction, hence the name compass plant. Areas where compass plants are found are assumed to be remnants of native prairie. However, compass plants may also occur in prairie plantings or reconstructed sites, such as Red Feather Prairie at Saylorville Lake. Blooms from July into September. Native to N. A.

Cup Plant
Silphium perfoliatum



Flowering heads have from 20 to 30 ray flowers surrounding a central cluster of conspicuous, yellow, disc flowers. Involucral bracts are few in number, broadly ovate, and prominent. Leaves are broadly ovate and arranged in pairs. The paired leaves are fused to each other at their bases so that they surround the stem, forming a distinctive "cup," which may hold rain water. Margins of the upper leaves have shallow teeth of rather uniform size. Lower leaves have large, prominent teeth, that are lobe-like and not uniform. The stem is square rather than round. This is a tall plant, growing shoulder high or higher. Blooms from July through September, in prairies and prairie plantings, where soil is damp. Native to N. A.

Fig. 1. Species descriptions of two wildflowers from the "Electronic Guide" as displayed in PDF format in the CD-ROM (Wacha 2001b).

for developing the online guide is to create a public awareness and appreciation of the wildflowers found within the Saylorville Lake Project and on adjacent public lands. It is hoped that the guide will contribute to this realization. How effective the website will be in achieving this goal, however, remains to be evaluated.

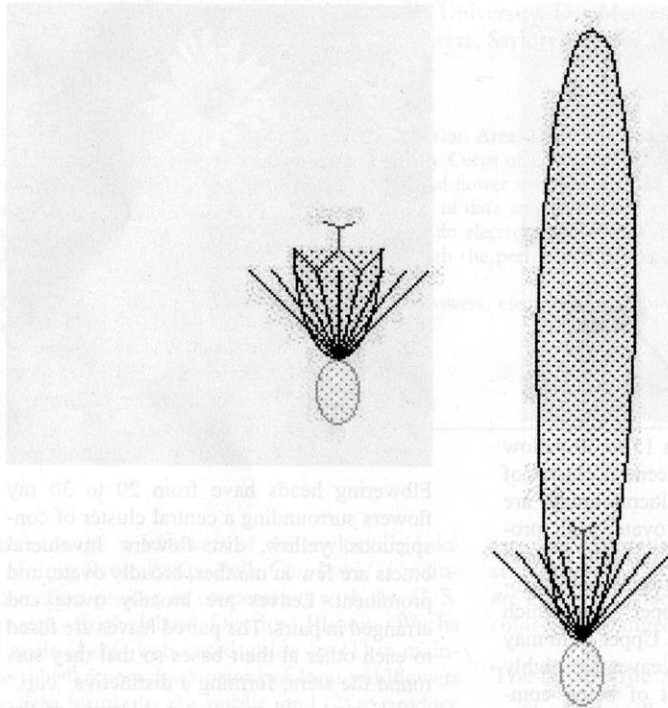
METHODS

Photographs of wildflowers were taken *in situ*, in the field, at the Saylorville Lake recreation site with the aid of a 35 mm camera using standard photographic methods. Bracketed exposures of wildflowers were made using *Kodachrome* or *Ektachrome* color-positive films. Images, selected from the resulting pool of photographic slides, were scanned into a *Macintosh* computer with the aid of a *Nikon Coolscan* slide scanner. Captured images were refined using *Adobe Photoshop*

3.0 software. These images were stored in JPEG format and imported into *Adobe PageMill* 3.0 for preparation of the web pages. All photographs constitute original work. Line diagrams of flowering parts (e.g., Fig. 2) were made using the graphics component of *Adobe FrameMaker* 5.0. The diagrams were converted to JPEG images in *Photoshop* prior to importing them into the *PageMill* program. The server is an *iMAC* (MHz 350; RAM 64) running *Quid Pro Quo* server software by Social Engineering [commercially unavailable at this writing]. A CD-ROM containing the Aster Family component of the online site was produced for publication (Wacha 2001b) using a *La Cie* 4 × 2 × 6 CD-RW writer. The Aster Family contents were copied to the CD-ROM from the online source in the *PageMill* program, which, when viewed on the CD-ROM, resembles the website in appearance and operation. A PDF document of the Aster Family

A Guide to Common wildflowers of the Aster Family in Central Iowa

Disc and Ray Flowers



Disc Flower (left). Ray Flower (Right)

Note: Disc flowers have 5 petals fused together to form a tube (blue). Ray flowers have 5 petals fused together, but they do not form a tube. Instead, the would be tube is "unfurled" to form a conspicuous, long, ribbon-like ray (blue). Below the petals is the ovary (green), which, upon fertilization, becomes a fruit, or "seed," called an achene. Positioned above the ovary is the pappus, a cluster of bristle-like filaments that facilitates wind blown dispersion of the achene. The stamens, or male parts of the flower, are contained within the tube of petals. They are not illustrated here. The stigma of the pistil, however, is illustrated, in red. The stigma is divided into two segments, and appears forked. It is connected to the ovary by a "style," which is not shown.

Fig. 2. Computer generated diagram of disc and ray flower of the Aster Family (with text legend as it appears in the "Electronic Guide" and in the PDF document from the CD-ROM (Wacha 2001b).

content was also prepared for inclusion in the CD-ROM. This document, which is arranged in a condensed two-column format including images and text, can be printed with a standard ink-jet printer on letter-size paper for use in the field (Fig. 1). The PDF document was created using the *FrameMaker* application and was converted to PDF with *Acrobat Writer* (Adobe). Descriptions of the wildflowers contained in the guide are based on flower specimens collected from within the Saylorville Lake Project area during the

course of the study. Specimens were collected with the permission of the U. S. Army Corps of Engineers and prepared according to standard herbarium methods (Woodland 1997). However, pressed specimens were not attached to herbarium sheets in order to facilitate their optimal arrangement for digital photography. Species identifications were determined in part with the aid of the following references: Barkley et al. (1987), Eilers and Roosa (1994), Gleason (1968), Steyermark (1963), and Van Bruggen (1958).

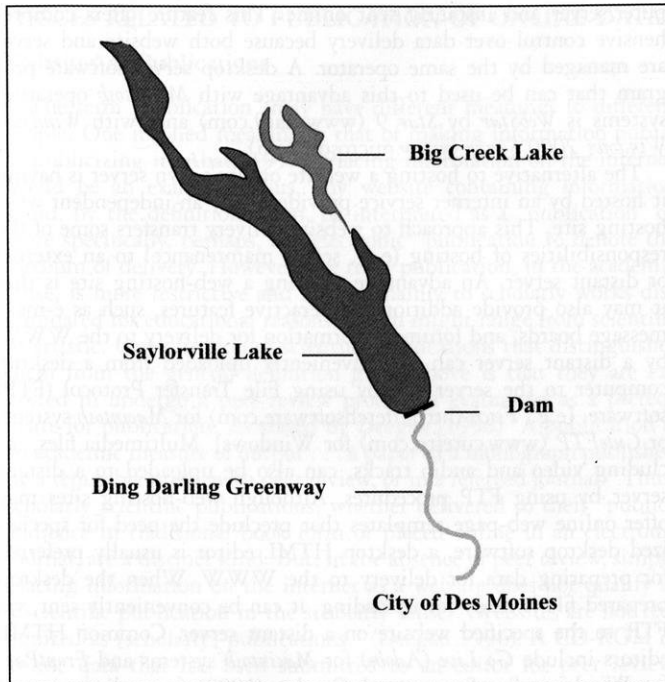


Fig. 3. Computer generated map showing the relationship between Saylorville Lake, Big Creek Lake, and the Ding Darling Greenway. The Ding Darling Greenway as shown extends 9 km south of Saylorville Dam and terminates within the city of Des Moines.

TRADITIONAL VS. ELECTRONIC GUIDE: A COMPARISON

Wildflower guides constitute a unique genre of information available to those interested in wildflower identification. Guides are typically directed toward identifying showy, herbaceous species (wildflowers) that have an aesthetic appeal and are characteristic of a particular habitat (e.g., prairies or woodlands) or a particular region or locality such as the Midwest or Saylorville Lake. An electronic guide represents a technological departure from the traditional guide. In this section, both types of guides are compared to illustrate their features.

The Traditional Guide

Traditional field guides are intended to facilitate the identification of wildflowers in their natural setting and to enhance an appreciation for wildflowers by the general public. The use of field guides by students and naturalists also points to their function as an educational resource for learning about flora. Field guides contain varying amounts of information that may include images of flowers, descriptive features, flowering periods, geographic distribution, ethnobotanical information, family characteristics, a glossary, a key to species, and references. This information varies in degree of complexity depending on the guide (compare: Edsall 1985, Grimm and Kartesz 1993). The contents are usually moderately complex and of a general nature, describing a limited number of showy species within a defined geographic location. This is in contrast to either a floristic study or a flora (e.g., Barkley et al. 1987), which are more detailed in content and concerned mainly with a systematic evaluation of all plants in a given taxon or geographic region for scientific rather than public purposes. Because the traditional field guide is distributed as

a book or manual, it is highly portable, and because it is printed on paper, it is relatively permanent in archival quality.

The Electronic Guide

An electronic guide, served online, is similar to a traditional guide in that it contains images and descriptions of wildflowers along with related information such as distribution of species, etc. However, the electronic guide differs in several ways:

Electronic guide as an open-ended database. One difference inherent in an electronic guide is the capacity to modify the data within the guide. In the traditional guide, the data are fixed and cannot be modified without creating a new edition because the contents are printed in book form. In the electronic guide, the data are not fixed and can be modified at any time because there is continuous access to the html editor, from which the guide is being electronically served. Thus, data can be expanded or changed as needed to include additional species, images, descriptions, diagrams, or corrections and enhancements. Because of this capacity to modify data, the online guide may be thought of as an "open-ended" database (Moffett 1996). Conversely, due to its "fixed" or indelible format, the traditional guide may be considered as a "closed" database in the context of its currently published edition.

Portability. A second distinction is portability. A traditional guide can be transported effortlessly into the field. An electronic guide, however, is tied to a computer screen and can be accessed in the field only through a remote connection (e.g., via a cell phone connected to a laptop computer). Direct use of an online data source in the field, therefore, is complicated by the technological requirements of the system. But, with the "wireless-web" features of small-screen "palmtops," it should become increasingly handy to have direct access. However, "indirect" access to online information is available, either by CD-ROM used with a laptop computer, or by a printed PDF document that can be used in the field with the same convenience and effectiveness as a traditional guide.

Access to the medium by which the information is delivered. Although the content and purpose of both the traditional and online guides may be somewhat similar, use of the online guide requires a working knowledge of computers and access to the internet that a traditional guide does not. If computer-use were to become universal, however, the traditional guide might still retain its value through its practicality in the field and self-contained format.

Format by which the information is presented. Traditional guides are printed in book form. Their format is restricted mainly to pictures, diagrams, and text. With an online guide, the electronic format is unrestricted and, along with standard images and text, can accommodate video information and direct links to other sites. Therefore, it has multimedia capability. Online information can also be transferred to a CD-ROM or a magnetic disc for offline use.

Archival qualities. As stated by Hedstrom (1998), "The purpose of preservation is to protect information of enduring value for access by present and future generations." Printed media are relatively long-lasting. For example, acid-neutral paper may last a century and more (Hedstrom 1998). This quality of "permanence" is an advantage for traditional guides printed on paper. Electronic media are more labile. Magnetic media are subject to binder degradation, particle instability, and substrate degradation (Hedstrom 1998). These media (floppy disks, 100 MB disks, etc.) have life spans of 10–30 yrs if properly stored (Hedstrom 1998). Optical disk media (CD-ROMs, DVDs) are subject to high humidity, extreme temperature fluctuation, and contamination by airborne particulates, but if properly stored they may reach a lifespan of up to 100 yrs (Hedstrom 1998). These considerations are important not only when backing-up online databases to guard against loss or damage, but also in preserving data for

archival reasons. Archival considerations are relevant, because the ultimate fate of an open-ended database (website) is either termination and withdrawal to storage or replacement with a new database (Moffett 1996).

Apart from the purely archival value of storing online data on magnetic or optical media, preserving or backing-up the database provides an electronic library of stored images, diagrams, and text that may be accessed later for use in other applications or in new databases. Hence, archived data not only become a matter of record, but also may have value for future use.

ISSUES ASSOCIATED WITH MAINTAINING AN ONLINE DATABASE

Several considerations are important in maintaining an online database, not the least of which are those relating to the expense and time involved in collecting, organizing, and maintaining information online. But, of additional importance, assuming these preliminary conditions have been satisfied, are management issues related to software and hardware upgrades, image enhancement, serving the data electronically, linking with other internet sites, and perhaps, incorporating video images. These are some of the routine issues of maintaining an online database presented here.

Upgrading Software and Hardware

As an electronic database ages, so too do the tools of electronic acquisition and delivery, which periodically require updating to maintain their effectiveness in the presence of newly-marketed tools. With the online guide, a different HTML editor, *Go Live* (www.adobe.com), is scheduled to replace the existing editor *PageMill*. Also photographic images are now being captured with a digital camera rather than a traditional one (Wacha 2000). Upgraded versions of *Adobe Photoshop* (v. 5.0) and *FrameMaker* (v. 5.5) have also been incorporated. With such changes, added costs may be expected to occur, especially for software upgrades. But, to improve effectiveness of online delivery, change may be necessary. Some expenses, however, may decline. In terms of hardware upgrades, for example, the cost of a digital camera may be less than that of a 35 mm slide scanner which it replaces, and operating costs for a digital camera may be lower than those of a traditional camera because neither film nor film-processing are required for image acquisition.

Image Enhancement

In preparing images for online use, an image editor (e.g., *Adobe Photoshop*) is especially helpful for enhancing contrast and brightness and for sharpening images. Sharpness is best achieved with the aid of the "unsharp" mask filter, which allows for graduated degrees of sharpness or "unsharpness" to be selected. The quality of images captured by digital camera or with the aid of a digital scanner can almost always be improved with these tools. The image editor is useful also for resizing and cropping images and for adjusting color quality. An advanced imaging editor, like *Adobe Photoshop*, is of primary importance for website development because it allows for the highest quality image outcome within the limitations of the medium. A comprehensive reference on digital imaging is that by Greenberg (1999).

Desktop and Distant Servers as Web-Hosting Sources

Use of a desktop computer as a server, from which to broadcast a database over the internet, is an advantage in that information delivered in this way can be modified as the need arises for immediate delivery on the WWW. Information to be added to a database can be conveniently typed into the HTML editor of one's desktop com-

puter/server and instantly sent online. This feature offers comprehensive control over data delivery because both website and server are managed by the same operator. A desktop server software program that can be used to this advantage with *Macintosh* operating systems is *WebStar* by *Star 9* (www.star9.com) and, with *Windows*, *Windows 2000 Server* (www.microsoft.com).

The alternative to hosting a website on one's own server is having it hosted by an internet service provider or by an independent web-hosting site. This approach to website delivery transfers some of the responsibilities of hosting (e.g., server maintenance) to an external or distant server. An advantage of using a web-hosting site is that it may also provide additional, interactive features, such as e-mail, message boards, and forums. Information for delivery to the WWW by a distant server can be conveniently uploaded from a desktop computer to the server site by using File Transfer Protocol (FTP) software, [e.g., *Fetch* (http://fetchsoftware.com) for *Macintosh* systems or *CuteFTP* (www.cuteftp.com) for *Windows*]. Multimedia files, including video and audio tracks, can also be uploaded to a distant server by using FTP procedures. Although web-hosting sites may offer online web-page templates that preclude the need for specialized desktop software, a desktop HTML editor is usually preferred for preparing data for delivery to the WWW. When the desktop prepared file is ready for uploading, it can be conveniently sent, via FTP, to the specified website on a distant server. Common HTML editors include *Go Live* (*Adobe*) for *Macintosh* systems and *FrontPage* for *Windows*. See Sawyer and Greeley (1999) for a discussion of distant servers and Tauber and Kienan (1997) for hosting and managing websites.

Links to External Sites

Adding internet links to connect external websites to an online database serves to expand the overall database for users. These links may be thought of as electronic analogs to the bibliographic references listed by traditional guides. Linked, external sites are helpful, too, in that they may serve as models for data formatting or site navigation. One such model for an online wildflower database is that maintained by the California Academy of Sciences (2001).

Video Images

One reason for presenting wildflowers in video format is to demonstrate them in realistic perspective as viable objects in their natural setting moving with the wind in concert with nature. This reason may not replace the advantage of the static image for taxonomic identification, but it does provide a realistic impression of a plant that may help to interpret it for the viewer. In essence, the video image takes the viewer into the field.

Video images of wildflowers can be captured with either an analog or digital video camera. Video clips can be prepared for online delivery by using video editing software (e.g., *Adobe Premiere*). Analog images must first be converted to digital ones. A program capable of achieving this conversion for the *Macintosh* platform is *Interview* by *XLR8* (www.xlr8.com). A video editor that is packaged with *Interview*, or available separately, is *Videoshop* by *Strata* (www.strata.com). Online videos are commonly viewed with *Quick Time Player* (www.apple.com), a cross-platform program for *Macintosh* and *Windows*. A principal consideration in broadcasting videos online is file size, which must be kept small to facilitate realistic downloading times for viewing. However, file size is less of a consideration if video clips are to be incorporated into a database on CD-ROM, where they can be viewed directly without having to wait for downloading. For an account of video editing see Stern and Lettieri (1999).

ISSUES RELATED TO PUBLICATION OF ONLINE DATA

Websites as Publications

The term "publication" may have different meanings to different people. One implied meaning is that of making information public or publicizing it (Abate 1997). Placing information on the internet would be an example. Thus, any website containing information could, by the definition given, be interpreted as a "publication" or more specifically, perhaps, an "electronic" publication to denote the medium of delivery. However, the term publication, in the academic sense, is more restrictive and applies mainly to scholarly works disseminated for educational reasons, which might range from scientific to artistic. One criterion of scientific publications that distinguishes them from the general definition given above is that they are expected to undergo a peer review process of evaluation as a prerequisite for publication. As stated by Deegan (1996) "A publication is an academic measure of output . . . a paper in a monograph published by a reputable press, with peer review, or in a refereed journal." Thus, scholarly scientific publications, whether delivered to their "public" audience in traditional book form or placed online in an electronic journal, are a distinct kind. But, in the absence of peer review, simply placing information on the internet as a website does not qualify as a scientific publication in the scholarly sense: "Websites are not recognized as [scholarly] publications." (Deegan 1996). A CD-ROM of online data that has been submitted to an editor for peer review, however, may qualify: "CD-ROMs are of the same interest to scholars as books, and may be accessible in the same areas of a library." (Deegan 1996).

This is not to suggest that scientific information presented online does not meet publication standards. It may or it may not. But in the absence of peer review, it cannot be guaranteed that a website is maintaining the standards expected of a peer-reviewed publication.

CD-ROMs and PDFs as Publications

One way that an author of a website may meet publication standards is by submitting the online database, in parallel fashion, for publication as an "offline," peer-reviewed CD-ROM or as a peer-reviewed PDF file which can be delivered "online." Both the CD-ROM and PDF documents can serve as closed databases, the content of which, like that of a traditional guide, will remain unchanged until resubmitted to a publisher for revision. This method of achieving publication standards for electronically-served information retains, for the electronic medium, the publication value of the "closed" database.

CD-ROMs have further value in their capacity to serve an archival function. As reservoirs of stored data, the information they contain may be retrieved as needed for use in other applications. Production of CD-ROMs appears to be increasing each year in multiple areas of interest, including academic (Brown 1996).

Modes of Electronic Publication

Two distinct approaches (modes) for presenting electronic data seem apparent: one is the open-ended, non-reviewed database and the other, the closed, but reviewed database. Eysenbach (2000) categorized these two approaches to publication as being either a "Type 1" publication (the open-ended, non-reviewed category) or a "Type 2" (the closed and reviewed category). Delivery of the wildflower guide online, as a website, represents a Type 1 publication; the published CD-ROM of the Aster Family, taken from the website, represents a Type 2. Eysenbach's (2000) review of the impact of electronic publishing on biomedical research provides insight into the value of both types of publication. In his paper, it is also interesting

to note the similarities between his definitions of publication and that which we present.

FURTHER STUDY

With increasing use of the internet as an information system, focusing internet resources on our natural areas would appear to be a positive way to connect the public with local lands that we as environmental stewards hope to preserve and restore. The informational value in offering website access to our natural areas for aesthetic and environmental reasons seems self-evident. However, the extent to which delivery of electronic information does, in fact, fulfill this objective for our website remains obscure. For example, the online guide to wildflowers has a population of visitors who "log-on" to the website daily. But the demographic structure of this population remains unknown. This kind of information would be of value for measuring how effective we may be in realizing our perceived informational goals. Assessing this information through studies that focus on the educational value of our website is a logical extension of this work that we hope to pursue.

SUMMARY

With the access available to internet service providers and the ease of using HTML editors to create websites, the opportunity to develop an online database is becoming increasingly practicable. Through a review of some of the issues related to online delivery, perhaps this paper can provide information of value for establishing and maintaining an online system that will focus on our natural areas. Hopefully, recreation users with access to this kind of information will develop a deeper awareness and appreciation for our natural areas and the work of conservation organizations and managers.

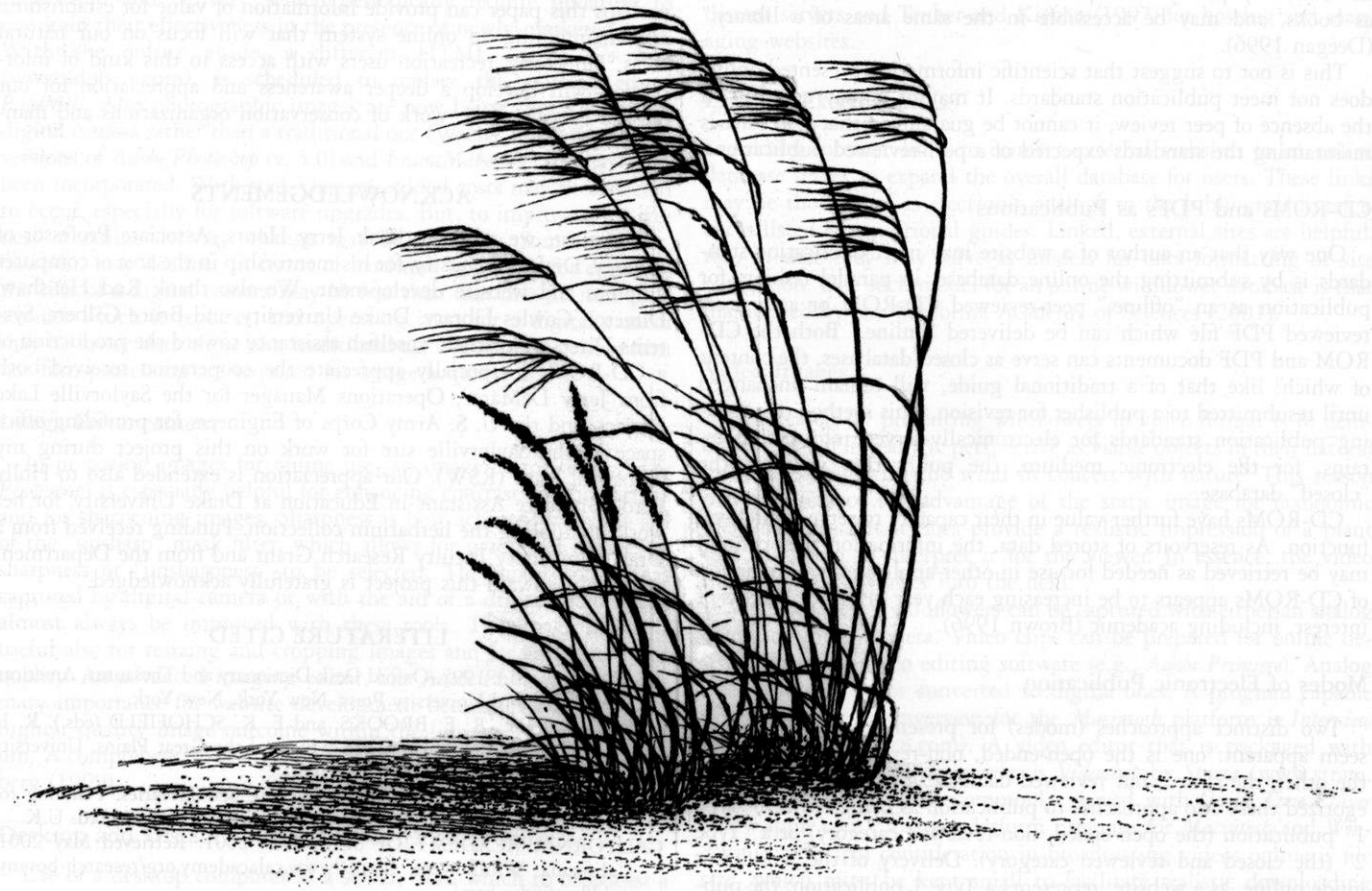
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The Center for Prairie Studies at Grinnell College: An Interdisciplinary Program in Place-Based Education

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The newly created Center for Prairie Studies at Grinnell College in Grinnell, Iowa, promotes integrative learning about natural and cultural aspects of the tallgrass prairie region in the past as well as the present. Intended to counteract a tendency among academics to underrate the significance of place in human life, the Center attempts to draw student and faculty attention to the region in which we are situated through hands-on learning in courses and through extra-curricular symposia, artistic events, and programs. The Center's mission includes an outreach component to the local schools, the community of Grinnell, and the region. The Center's activities are described, and a preliminary evaluation is offered.

INDEX DESCRIPTORS: interdisciplinary studies, prairie education.

A Center for Prairie Studies, dedicated to increasing the awareness, appreciation, and understanding of nature and culture in the tallgrass prairie region of North America, was established in the 1999–2000 academic year at Grinnell College in Iowa. Our central theme is the region's ecological character and its transformations due to human activity. The Center promotes interdisciplinary study of all aspects of this subject with several pedagogical purposes in mind: to teach our students that local knowledge is a route to general knowledge; to offer students more opportunities for hands-on learning; to increase students' knowledge of the region where they are attending college; to promote interdisciplinary thinking; and to promote research about the prairie region. The Center's mission also includes a collaborative outreach to a wider community, trying to reestablish a badly eroded connection to our natural landscape, as well as outreach to the primary and secondary schools, where building new understandings must begin.

In this paper, I briefly present an argument for place-based education, review the goals of the Center in more detail, describe the activities and programs that the Center has implemented, and offer a preliminary assessment of their success.

SLIGHTING THE LOCAL AND UNDERRATING PLACE

The creation and planning for the Center for Prairie Studies was sparked in part by our concern that many colleges and high schools fail to include studies of their own locales in their curricula. For example, reflecting back on his own education in Minnesota public schools in the 1950s, Paul Gruchow (1995) wrote in *Grass Roots: The Universe of Home*:

Among my science courses I took two full years of biology, but I never learned that the beautiful meadow at the bottom of my family's pasture was remnant virgin prairie. We did not spend, so far as I can remember, a single hour on the prairies—the landscape in which we were immersed—in two years of biological study.

Nature writer Lisa Knopp (1996) offered a similar observation about a disregard for local history while she was growing up in Iowa:

Gradually, I saw Burlington as the end of the world where nothing ever had happened or ever would. Certainly, what I learned in school reinforced, perhaps created, this attitude. American history seldom happened in my part of America; world history never happened in my part of the world. Since local history wasn't valued and thus wasn't taught (or vice versa), I learned little about where I was from and what it meant to be shaped by such a place.

The neglect of locale may have been ameliorated by the "Roots" phenomenon of the 1970s, but it certainly remains. Traveling through the Flint Hills of Kansas last year, I met a young woman who had grown up there, and I asked her how much she had learned in high school about the prairie and local history. "You want to know the truth?" she replied. "Nothing at all." Then after a pause she added, "It's really pathetic, when you think about it."

Similarly, many colleges do little to promote a connection between their students and the environs beyond the campus or to promote an awareness of the significance of place in human life in general. Eighty-four percent of the students at Grinnell College come from out of state, yet until two years ago the college did not offer a single course on local or regional history, literature, ecology, society, or the arts. As a consequence, most students graduated after four years knowing little more about Grinnell, Iowa or the rural Midwest than when they arrived. Colleges which do offer such courses rarely promote them as special components of their curricula. Eric Fency (1996) pointed out that "as citizens of the *cosmo polis*, the mythical 'world city,' professors are expected to owe no allegiance to geographical territory; we're supposed to belong to the boundless world of books and ideas and eternal truths, not the infinitely particular world of watersheds, growing seasons, and ecological niches." Professors train their students to believe that little of interest happens locally, that the truly important lessons transcend place, and, ultimately, that place is insignificant. An attitude favoring the study of ideas over places has virtually become part of the academic subculture.

The young woman in Kansas sensed a flaw in this approach to learning even if she could not fully articulate what it was. Fortunately, recent scholarship in diverse fields is beginning to explore

the importance of a connection to place. Kent Ryden (1993) wrote about the way in which familiarity with a place—a landscape and its inhabitants—is reflected in folklore and shapes the ways people from that place think, feel, and perceive the rest of the world. In collections of essays edited by Hannum (1997), Williams et al. (1998), and Barnhill (1999), the authors linked a sense of place to, among other things, spirituality, conservation-mindedness, health, faith, wise agricultural practices, ethnic identity, self-identity, and community. The message is clear: neither “nature” nor “culture” can be separated from a spatial context. To ignore the specific character and history of your particular place in the world is to cut yourself off from a unique base, grounding, and touchstone.

One of the principal goals of the Center for Prairie Studies is to convince students and faculty that local events are significant, and important lessons are connected to place. We advocate “place-based education.” This approach to learning flies in the face of standardized curricula and standardized testing, and it is so uncommon that its absence might not be readily noticed. Place-based education begins with the premise that one’s locale can be an excellent classroom. Knowing about where you live—both its natural and its cultural character, the environment and the community—helps you live there more wisely. If you not only feel *in* a place but *of* it as a result of knowing it well, you might take better care of it. Anthropologists generally believe that Native Americans, whose education was pointedly place-based, understood they were a part of their locale and, as such, needed to care for it. Understandably, European settlers did not know the prairie as well as the Native Americans whom they displaced. They brought with them different knowledge and a different agriculture which, though enormously productive, has been incompatible with the sustainable use of the prairie. They lacked what the anthropologist Clifford Geertz (1983) called “local knowledge,” and only now, after a century and a half, are we beginning to gain it.

Place-based education provides an opportunity for students to experience their locale directly and unmediated by someone else’s written words and begin to build on their local knowledge. You can go into a prairie, forest, or desert, or into a neighborhood, market, or factory and use all of your senses to learn from what is there. This “hands-on” learning, or as the faculty associated with the Center prefer to call it, “discovery mode learning,” is inherent in place-based education and has significant pedagogical value. As an historian in our program commented, “I can teach my students about the Great Depression by having them read documents, but I can also send them into town to interview people who lived through it. Do you want to bet which they learn more from?” Many of our students have confirmed the value of this kind of learning in written course evaluations.

In response to students’ perceptions that the really important things are happening elsewhere, the faculty associated with the Center maintain that many important things have happened and are happening here in the prairie region. The loss of biodiversity, the rise of biotechnology, changing gender relations, artistic creativity, evolution, debates about the teaching of evolution, multiculturalism, and technological innovation are only a few of the important topics that can be studied through a prairie focus. Our faculty suspect that the “breaking of the prairie” in the mid-nineteenth century was the most extensive and rapid human destruction of an ecosystem at any time in human history and would warrant study in *any* curriculum. As these examples suggest, place-based education need not be parochial. The study of our locale can also instruct about more general principles and theories. Geertz (1973) once wrote, “anthropologists don’t study villages; they study *in* villages,” and then they cautiously attempt to extrapolate the “general relevance” from the particular case. Even though our students may leave Iowa and the prairie re-

gion, the importance of forming a connection to place, like the knowledge of biological principles, is transferable.

PROGRAMS AND ACTIVITIES AT THE CENTER FOR PRAIRIE STUDIES

The Center for Prairie Studies advocates an interdisciplinary approach to the study of place. The prairie seems especially promising in this respect because nature and culture have long been intertwined. It is generally held that fire intentionally set by humans played a crucial role in maintaining the prairie for thousands of years (Collins and Wallace 1990). Prairie can be considered, at least in part, an anthropogenic landscape. The destruction of the prairie in the nineteenth century at the hands of European settlers, and the efforts today to preserve and reconstruct prairie ecosystems, illustrate the on-going role of humans. Therefore, to understand the prairie we need to understand not only climate, soils, plants, and animals, but also human knowledge, values, adaptive strategies, political systems, and beliefs. Many fields of study must be involved, and it is not surprising that much of the most engaging analysis of the prairie region over the years incorporated knowledge from several disciplines in their work, from the early studies of Aldo Leopold (1949), May T. Watts (1957), and James C. Malin (collected in Swierenga 1984), to the more recent work of John Madson (1982), William Least Heat-Moon (1991), Richard Manning (1995), and the essay collections edited by Robert Sayre (1999) and A. Dwight Baldwin, Jr. (1994).

The faculty affiliated with the Center for Prairie Studies are also drawn from a diversity of disciplines, including anthropology, art, biology, economics, geology, history, literature, music, political science, religious studies, sociology, and theater. Many have already developed new courses or course components in their departments that deal with prairie themes, and there will be increased prairie-related offerings in the future. The faculty associated with the Center believe that exposure to local history and our prairie region in one subject area will stimulate students to pursue studies of our region through other disciplines. For example, a student who learns about the prairie in a literature course by reading Willa Cather or Hamlin Garland may decide as a result to take a course in prairie biology, or a student who studies the geology and geography of the region may become interested in the effect that the landscape and local materials had on Prairie School architects such as Frank Lloyd Wright and Walter Burley Griffin.

Brief descriptions of a few of the courses developed with the Center’s encouragement can illustrate the kinds of learning being encouraged. Jackie Brown, Associate Professor of Biology, offers a section of introductory biology called “Prairie Restoration.” He finds that he can teach the principles of evolutionary ecology, genetics, systematics, and population biology using prairie as his example and laboratory. For two years, Brown’s students have carried out numerous research projects on various aspects of prairie restoration at the college’s Conard Environmental Research Area (CERA). Their reports are published in annual editions of an in-house journal, *Tillers: A Journal of Prairie Restoration Research*. By studying tallgrass prairie, Brown’s students learn principles relevant to other geographical contexts and applicable in more advanced courses. From the standpoint of prairie studies, their learning experiences have been enriched by studying the place.

A second example comes from a series of classes on printmaking taught by Professor Tony Crowley of Grinnell’s Art Department. Crowley’s openness to combining perspectives from different disciplines grows out of his interest in synesthesia, a phenomenon in which one type of sensory stimulation evokes the sensation of another. In his printmaking classes, Crowley has not only taken his

students to local prairies to experience them esthetically, but has invited biologists and creative writers to visit the class and talk about the ways they perceive prairie and communicate about it. He found that these contacts affected how his students saw and interpreted the prairie in their artwork. In addition, he required them to write about the prairie and thus to work in two creative mediums at once. The students' artwork was exhibited on campus, and their writings were published in a booklet titled *The Prairie: Sound, Vision, Substance*. Students seemed to take their art and writing assignments more seriously knowing that their work would be exhibited and published.

The Center has supported other models for interdisciplinary teaching. Last year, a colleague in the music department, Jonathan Chennette, and I designed our two first-year tutorials to complement one another. His was called "The Prairie Landscape in the Arts" and emphasized painting, music, and literature; mine was "Prairie Encounters," a social-cultural history of the prairie region. We selected only a few readings in common, but we arranged our syllabi so that we discussed similar thematic topics—among them Native Americans, early pioneer settlements, the challenge of farming in the Depression, and the decline of the family farm—at the same time. Our classes met together eight times during the semester (including one field trip to Neal Smith National Wildlife Refuge), and on these occasions our discussions were enriched by the different perspectives the two groups of students brought with them.

In addition to supporting prairie-related courses and course components, the Center for Prairie Studies is engaged in other activities that promote an awareness and understanding of the prairie region. The Center has sponsored or co-sponsored guest speakers, symposia, and workshops on diverse topics, including, "An Agriculture Where Prairie is the Measure," "Walter Burley Griffin and Prairie-Style Architecture," a "Sedge Identification Short Course," and "The Art of Living With the Land" (at which two farmers, one also a poet and the other also a photographer, shared their poetry and photography as well as their practical connections to the land). The Center has also brought two art exhibits to campus. One exhibit highlighted artwork by contemporary artists who deal with themes of natural and transformed prairie landscapes. The other exhibit, of historic farm photographs, has evoked memories in visitors who grew up on farms and stimulated the curiosity of others who do not have a farming background. In the future, the Center hopes to sponsor musical and theatrical events as well. The Center provides stipends for three summer internships by Grinnell College students to explore prairie-related issues in a variety of settings. In previous summers, interns have worked at Living History Farms in Des Moines, Iowa, the office of North Dakota Senator Byron Dorgan in Washington, D.C., and the Neal Smith National Wildlife Refuge near Prairie City, Iowa.

The Center's outreach to the community of Grinnell and beyond is multifaceted. Examples include: a co-sponsored speaker series on ethnicity in Iowa with the Grinnell Historical Museum Society, field trips and instructional support materials to children in the public schools, field trips for community members to local prairies and farms, and *A Guide to Prairie Sites Near Grinnell, Iowa*, to help people find and explore prairies at their own pace and in their own way. The Center continues to support a local food-buying initiative at the college and the establishment of a community-supported agriculture program in Grinnell. For more detailed descriptions of our programs, please visit our website at www.grinnell.edu/cps.

OUTCOMES

It is still too early to fully assess how well the Center is accomplishing its mission. The faculty of the Center are encouraged by the level of interest in our programs on the part of students, faculty, and

community members. Our recent three-day symposium, "Revitalizing Family Farms and Rural Communities," drew a diverse audience of 50–100 people at each of seven events. Students are enrolling in courses with prairie studies components in respectable numbers. The level of interest in summer internships has been building. Several students have pursued independent study projects with various faculty members affiliated with the Center. One, a senior from Connecticut who did a project on the federal government's General Land Office Surveys in Iowa, said that he chose the topic because he wanted to learn something about Iowa before he graduated. Another, a senior from Washington state who took one of the printmaking courses mentioned earlier, wrote to her academic advisor about her class experience:

Today we were wrapping up our section inspired by visiting Krumm Nature Preserve . . . and I wanted to let you know I think our class experience was superb. Seeing the restored prairie was a powerful, transforming experience for all of us. We see our surroundings differently (and perhaps get closer to actually *seeing* and feeling what's around us), and we ache to be back out where we can observe wild things and the passage of time. Also, there was a general feeling from the class that we want to go back home and observe our more familiar surroundings with the same intensity. Rarely have I had a class assignment so enjoyable and so moving.

This is precisely the kind of thing that the faculty hoped for, and that Wes Jackson (1996) called for in his book, *Becoming Native To This Place*. Jackson advocated a college education which prepares students "to return home, or to go some other place, and dig in." Immersing ourselves in the local environment and local community is the necessary first step in learning how the world works and how to (and often *not* to) exist in it. "We will be *required*," Jackson (1996) wrote, "to become native to our little *places* if we are to become native to this *place*, this continent."

In conclusion, the Center for Prairie Studies at Grinnell College is attempting to foster an integrative, place-based, discovery-mode approach to learning about the natural and cultural aspects of the region we are in. At the Center, we use "prairie" in as much a metaphorical sense as a literal sense. We are interested in whatever has been and now is occurring in the tallgrass prairie region, especially in whatever is related to the land and our interactions with it and to the world views and values that shape and grow out of that interaction. We are interested in prairie populism and prairie-style architecture as much as prairie clover and prairie phlox, in artistic depictions of the prairie as much as scientific ones, and ultimately in learning to live intelligently upon the land.

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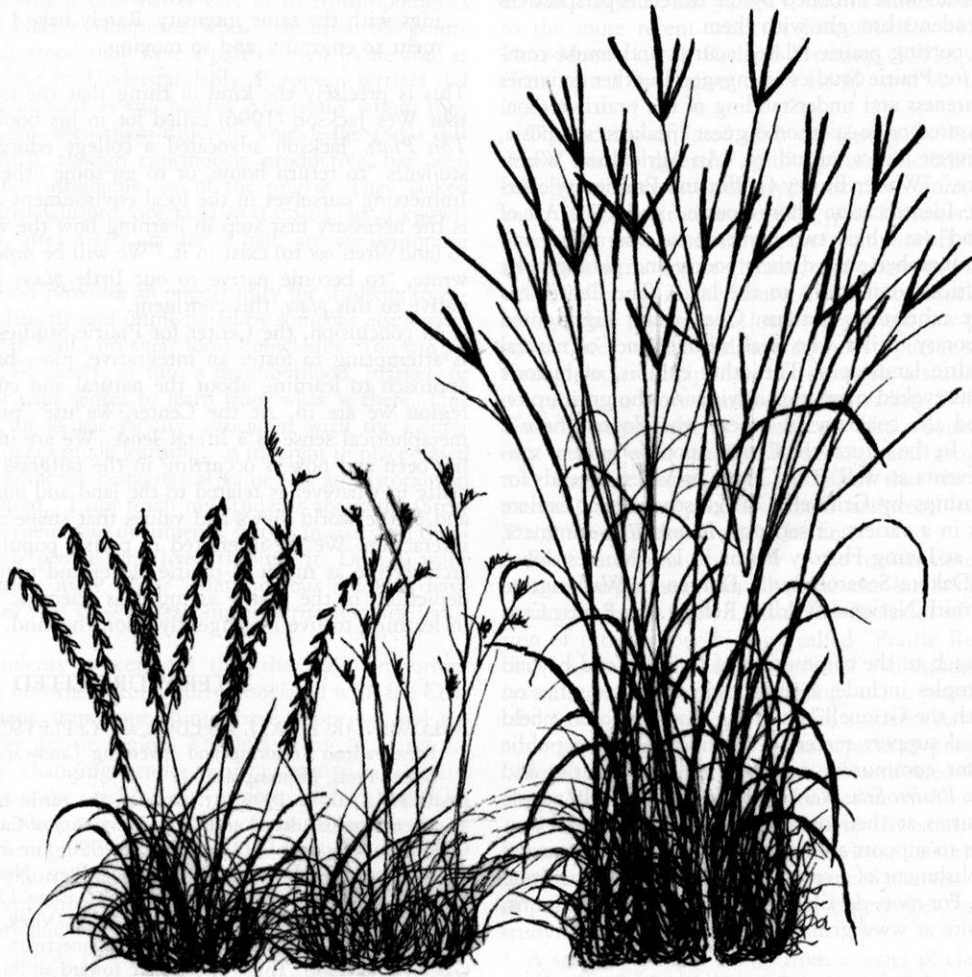
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Other Papers and Posters Presented

PAPERS

- Variation in mycorrhizal relationships during prairie restoration**
R. C. Anderson
Illinois State University, Normal, IL 62901-4120
- Conversion of over 90,000 cropland acres to wetlands and native upland cover**
J. E. Ayen and A. M. Ehley
210 Walnut Street, 693 Federal Building, Des Moines, IA 50309
- Soil resources control productivity and diversity in restored prairie**
S. G. Baer, S. L. Collins, J. M. Blair and A. K. Knapp
Kansas State University, Division of Biology, Manhattan, KS 66506
- Prairie school architecture in Mason City by Frank Lloyd Wright, Walter Burley Griffin and others**
P. Bang
North Iowa Area Community College, 500 College Drive, Mason City, IA 50401
- Small mammal populations in a school nature center**
D. Block
Worth County Conservation Board, 503 First Avenue North, Northwood, IA 50459
- Monitoring of prairie bushclover *Lespedeza leptostachya* in South-central Iowa**
P. J. Bockenstedt¹ and D. D. Smith²
¹ Bonestroo, Rosene, Anderlik & Associates, 2335 West Highway 36, St. Paul, MN 55113; ² University of Northern Iowa, Cedar Falls, IA 50614
- The effects of fire and climatic variation on the relative abundance of greater prairie chickens**
J. F. Cavitt and V. Nelson
Department of Zoology, Weber State University, 2505 University Circle, Ogden, UT 84408-2505
- Changes in vegetation at Herbert Hoover NHS reconstructed prairie: 1982-1999**
P. Christiansen
Cornell College, 600 First Street West, Mt. Vernon, IA 52314
- Habitat use and survivorship of headstarted ornate box turtles, *Terrapene ornata ornata* in Wisconsin**
R. A. Christoffel and R. Hay
University of Wisconsin, Department of Wildlife Ecology, Room 218 Russell Labs, 1630 Linden Drive, Madison, WI 53706
- "Lost" species of Ohio's prairie flora**
A. W. Cusick
Division of Natural Areas and Preserves, Ohio Department of Natural Resources, 1889 Fountain Square Ct., Columbus, OH 43224
- Restoring the Regal Fritillary butterfly (*Speyeria idalia*) and its host plant (*Viola pedatifida*) at Neal Smith National Wildlife Refuge**
D. M. Debinski and P. Drobney
Department of Animal Ecology, 124 Science II, Iowa State University, Ames, IA 50011
- Progress report on tallgrass prairie and savanna ecological restoration at Neal Smith National Wildlife Refuge in Prairie City, Iowa**
P. M. Drobney
Neal Smith National Wildlife Refuge, P.O. Box 399, Prairie City, IA, 50228
- Rationale for local ecotype seed use in prairie plantings and development of an Iowa and Minnesota ecotype zone map for U.S. Fish and Wildlife Service seed production project areas**
P. M. Drobney
Neal Smith National Wildlife Refuge, P.O. Box 399, Prairie City, IA, 50228
- Two invasive annuals as indicators of range condition in tall-grass prairies in Kansas**
T. A. Eddy
Emporia State University, 1200 Commercial Street, Emporia, KS 66801
- Voluntary protection of land: our rights, our responsibilities**
M. Ehresman and J. McGovern
Iowa Natural Heritage Foundation, 505 Fifth Avenue, Suite 444, Des Moines, IA 50309
- The control of infiltration as a mechanism for the self-regulation of prairie ecosystems: Preliminary studies at Rolling Thunder Prairie State Preserve, Warren County, Iowa**
S. H. Emerman
Department of Biology and Environmental Science, Simpson College, Indianola, IA 50125
- Native prairie islands joined to create a mini landscape and a preserve for local prairie species at a northeast Iowa hill prairie**
R. Hamilton
22755 Hwy 64, Maquoketa, IA 52060
- Native prairie management guidelines and techniques**
R. Hamilton
22755 Hwy 64, Maquoketa, IA 52060
- The politics of invasive species**
Bonnie Harper-Lore
Federal Highway Administration, Washington, DC 20590
- Effects of an aqueous smoke extract on the germination of select tallgrass prairie seeds**
M. F. Hammer and K. A. Strait
Biology Department, Wayne State College, Wayne, NE 68787
- Bringing prairie to the public**
S. R. Johnson and M. V. Stark
Central College, 812 University Street, Pella, IA 50219

Internet prairie education offerings from Fermilab

B. Jokiel and B. Fraccaro
Fermilab, % 256 St. Andrews Drive, Bolingbrook, IL 60440

Monitoring breeding birds of a large-scale tallgrass prairie restoration in Iowa

E. E. Klaas and L. Hyde Thomas
Iowa Cooperative Fish & Wildlife Research Unit, Iowa State University, Ames, IA 50011

Flora inventory at Spring Creek Prairie: the first step in prairie restoration/management

K. L. Kottas, G. L. Davis, R. B. Kaul and J. Stubbendieck
University of Nebraska-Lincoln, Department of Horticulture, 377 Plant Science, Lincoln, NE 68583

Development of experimental equipment to address the unique problems of harvesting and planting mixed tallgrass prairie seed

E. Kromray
546 Crestview, Ottumwa, IA 52501

Grandview Prairie Wildlife Management Area ecosystem restoration project

J. J. Lane, G. Mathis, T. Foti, S. Simon and D. Zollner
Arkansas Game & Fish Committee, 7004 Hwy. 67 E., Perrytown, AR 71801

Impact of 3-year spring burn cycles on ground beetles of original and reconstructed tallgrass prairies

K. J. Larsen
Department of Biology, Luther College, 700 College Drive, Decorah, IA 52101

Ecological determinants of long-term vegetation change in managed and unmanaged prairie remnants

M. K. Leach and M. L. Milbauer
UW-Madison Arboretum, 1207 Seminole Hwy., Madison, WI 53711

It's all in the timing: the influence of seasonal burning on the richness, diversity, and abundance of leaf beetle (Coleoptera: Chrysomelidae) species in native tallgrass prairies

D. G. Ledoux
University of Missouri-Columbia, Department of Entomology, 187 Agriculture Building, Columbia, MO, 65211

Wisconsin's Glacial Habitat Restoration Area (GHRA) project—10 years into a landscape scale habitat restoration program

E. C. Lobner and T. E. Lizotte
Wisconsin Department of Natural Resources, 1210 N. Palmatory St., Horicon, WI 53032

Remote sensing of Resaca Wetlands at the Palo Alto National Battlefield Historic Site, Cameron County, Texas

R. I. Lonard, F. W. Judd, J. H. Everitt, A. Mahra Yanez and M. M. Crawford
Department of Biology, University of Texas-Pan American, Edinburg, TX 78539

The Kellerton Bird Conservation Area—A plan to insure permanent habitat for greater prairie chickens and other grassland birds in southern Iowa

M. S. Moe and E. B. White
Iowa Department of Natural Resources (IDNR), Box 592, Mount Ayr, IA 50854

The impact of white-tailed deer foraging on forbs in a remnant prairie

D. L. Nelson and R. C. Anderson
Illinois State University, Normal, IL 61790

The effect of prescribed burning on the onset and development of plant disease epidemics on Iowa's tallgrass prairies

R. J. Percifield¹, T. Rosburg² and F. W. Nutter, Jr.¹
¹Iowa State University, Department of Plant Pathology, 351 Bessey Hall, Ames, IA 50014; ²Drake University, Department of Biology, Olin Hall, Des Moines, IA

Functional change on the northern prairies: using breeding bird guilds as indicators

T. A. Radenbaugh
Canadian Plains Research Center, University of Regina, Regina, SK S4S 0A2

Native plant demonstration gardens

T. Rogers, E. Howes-Vonstein and S. Holland
Hawkeye Community College, 1501 East Orange Road, Waterloo, IA 52701

Progress report for the prairie invertebrate biodiversity inventory: work in Wisconsin

S. B. Sauer, E. D. Maurer, R. A. Henderson and R. A. Bautz
Wisconsin Department of Natural Resources Research Center, 1350 Femrite Drive, Monona, WI 53716

Prairie education through the humanities

M. V. Stark and S. R. Johnson
Central College, 812 University St., Pella, IA 50219

Germination of threadleaf sedge from the northern mixed prairie

G. Tichota¹, J. Stubbendieck¹ and R. Hiebert²
¹University of Nebraska-Lincoln, P.O. Box 830915, Lincoln, NE 68583-0915; ²Northern Arizona University, P.O. Box 5765, Flagstaff, AZ 86011-5765

Using imazapic to eliminate tall fescue in native prairie barrens

B. E. Washburn, T. G. Barnes, C. C. Rhoades and R. Remington
Department of Forestry, University of Kentucky, Lexington, KY 40546

A new paradigm for prairie management

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Seedling emergence and mortality of prairie forbs in an established stand of warm and cool season grasses

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University of Northern Iowa, Department of Biology, Cedar Falls, IA 50614

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Moorhead State University, Department of Biology, Moorhead, MN 56563

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Vegetation mapping at Badlands National Park, South Dakota

S. Dingman and J. Von Loh
National Park Service, Badlands National Park, P.O. Box 6, Interior, SD 5775

Wetland seed dispersal potential of ducks

M.L. Holt¹ and A.G. Van Der Valk²

¹Natural Resources Conservation Service, 115 2nd Ave., NW, Hampton, IA 50441; ²Iowa State University, Department of Botany, Ames, IA 50010

Increase of native germplasm from the Nature Conservancy of Texas, Clymer Meadow Preserve

M. J. Houck, J. Alderson and J. Edison

USDA-NRCS Plant Materials Center, 3776 FM 1292, Knox City, TX 79529

Development of native forb and legume germplasm at the Bismarck Plant Materials Center

M. J. Knudson, W. L. Duckwitz, N. K. Jensen, and D. A. Tober
USDA-NRCS Plant Materials Center, 3308 University Drive, Bismarck, ND 58504

Grazing management of Eastern Gamagrass in southwest Georgia

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A prairie mosaic: an atlas of Nebraska's land, culture, and nature

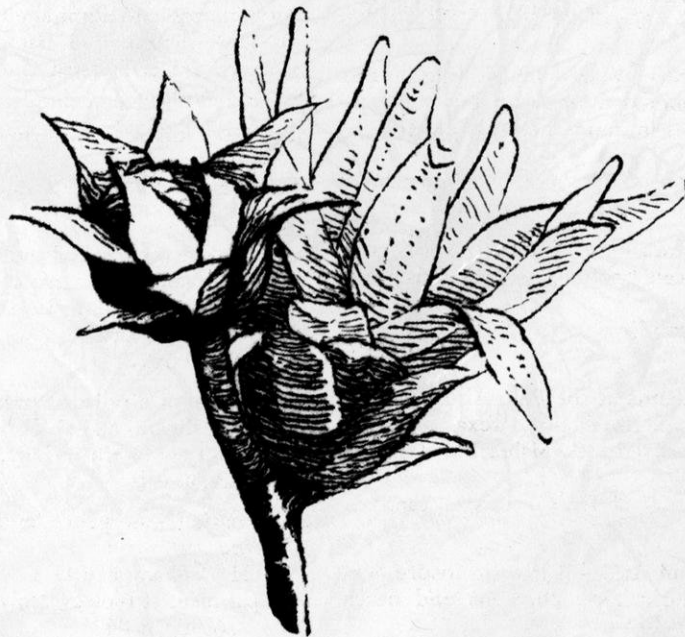
S. J. Rothenberger and S. George Bloomfield
Departments of Biology and English, The University of Nebraska at Kearney, Kearney, NE 68849-1140

Mead's milkweed, *Asclepias meadii* Torr.: the next step

J. M. Row, R. L. Wynia, T. C. Conway, and K. Kindscher
USDA-Natural Resources Conservation Service, Manhattan, KS 66502

The relative effects of soil and shade stress on taxonomic and morphological diversity in blackland prairie plant communities

E. Weiher, J. B. Grace, T. Schauwecker and S. Forbes
Department of Biology, University of Wisconsin-Eau Claire, Eau Claire, WI 54702



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- 10th**
22-26 June
1986
Texas
- Davis, Arnold, and Geoffrey Stanford, Editors. 1988. *The Prairie: Roots of Our Culture; Foundation of our Economy: Proceedings of the Tenth North American Prairie Conference*. Native Prairie Association of Texas, Texas Woman's University, Denton. 334 pages. [For copies, make checks for \$35.50 (U.S.) postpaid payable to: Native Prairies Association of Texas, P. O Box 210, Georgetown, TX. 78627.]
- 11th**
7-11 August
1988
Nebraska
- Bragg, Thomas B., and James Stubbendieck, Editors. 1989. *Proceedings of the Eleventh North American Prairie Conference*. University of Nebraska, Lincoln. 292 pages. [For copies, make checks for \$15.00 (U.S.) postpaid payable to: UNO Biology Department. Send to 11th North American Prairie Conference, ATTN: Tom Bragg, Department of Biology, University of Nebraska at Omaha, Omaha, NE 68182-0040.]
- 12th**
5-9 August
1990
Iowa
- Smith, Daryl D., and Carol A. Jacobs, Editors. 1992. *Proceedings of the Twelfth North American Prairie Conference: Recapturing a Vanishing Heritage*. University of Northern Iowa, Cedar Falls. 218 pages [For copies, make checks for \$18.00 (U.S.) postpaid payable to: Director, Prairie Institute. Send to Native Roadside Vegetation Center, University of Northern Iowa, Cedar Falls, IA 50614.]
- 13th**
6-9 August
1992
Ontario
- Wickett, Robert G. , Patricia Dolan Lewis, Allan Woodliffe, and Paul Pratt, Editors. 1994. *Proceedings of the Thirteenth North American Prairie Conference: Spirit of the Land, Our Prairie Legacy*. Department of Parks and Recreation, Windsor. 272 pages. [For copies, make checks for \$20.00 (U.S. or Canadian) postpaid payable to: Ojibway Nature Center. Send to Department of Parks and Recreation, 5200 Matchette Road, Windsor, Ontario Canada N9C4E8.]
- 14th**
12-16 July
1994
Kansas
- Hartnett, David C., Editor. 1995. *Proceedings of the Fourteenth North American Prairie Conference: Prairie Biodiversity*. Division of Biology, Kansas State University, Manhattan. 257 pages. [For copies, make checks for \$30.00 (U.S.) payable to: KSU Division of Biology. 66506]
- 15th**
23-28 Oct.
1996
Illinois
- Warwick, Charles, Editor. 1998. *Proceedings of the Fifteenth North American Prairie Conference*. Natural Areas Association, St. Charles. Natural Areas Association, P. O. Box 1504, Bend, Oregon, 97709. Out of print.
- 16th**
26-29 July
1998
Nebraska
- Springer, Joseph T., Editor. 1999. *Proceedings of the Sixteenth North American Prairie Conference: The Central Nebraska Loess Hills Prairie*. University of Nebraska at Kearney, Kearney. 263 pages. [For copies, make checks for \$25.00 (U.S.) postpaid payable to: Biology Department. Send to 16th North American Prairie Conference, ATTN: Dr. Joseph T. Springer, Biology Department, University of Nebraska, Kearney, NE 68849-1140.]
- 17th**
16-20 July
2000
Iowa
- Bernstein, Neil P., and Laura J. Ostrander, editors. 2001. *Proceedings of the Seventeenth North American Prairie Conference: Seeds for the Future; Roots of the Past*. North Iowa Area Community College, Mason City. [For copies, make checks for \$20.00 (U.S.) postpaid payable to: NIACC - Prairie. Send to Carol W. Schutte, North Iowa Area Community College, 500 College Drive, Mason City, IA 50401.]
- Future**
- 18th**
23-27 June
2002
Missouri
- "Promoting Prairie" Kirksville, Missouri, Contact person: Patricia A. Kelley
Kirksville Area Chamber of Commerce, 304 S. Franklin, Kirksville, MO 63501,
660-665-3766 phone.

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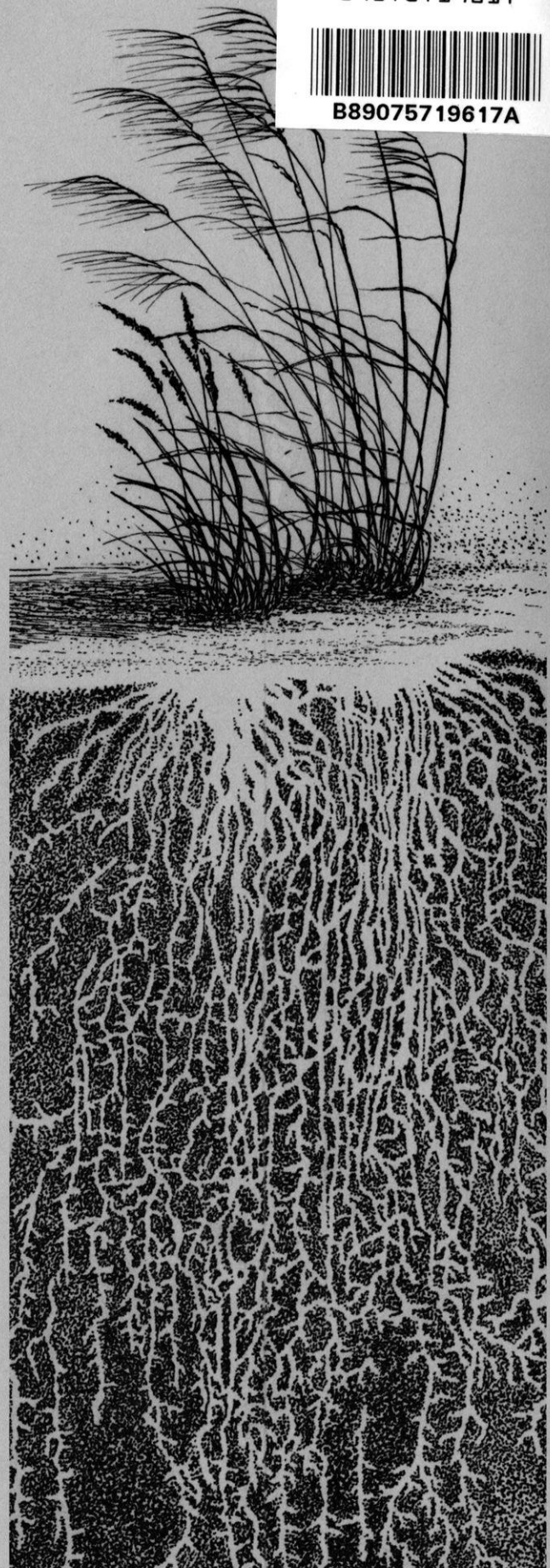
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