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PROCEEDINGS OF THE

EIGHTH NORTH AMERICAN PRAIRIE CONFERENCE

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Edited by Richard Brewer

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North American Prairie Conferences

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

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

Below are listed the published proceedings reporting each conference.

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

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

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

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

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

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

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

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

Public Prairies of Michigan

This 42-page, 8½ × 11 inch book was prepared in connection with the Eighth North American Prairie Conference by Kim Allan Chapman and Robert J. Pleznac. Its aim was to catalog "all grassland owned by organizations whose stated purpose is to preserve natural plant communities . . . and also sites on public land whether a designated natural area or not." Copies are available ($4.50 postpaid) from The Michiana Prairie Society, P.O. Box 667, Kalamazoo, Michigan 49005.

Proceedings of the Eighth North American Prairie Conference

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PROCEEDINGS OF THE

EIGHTH NORTH AMERICAN PRAIRIE CONFERENCE

1-4 August 1982 Western Michigan University Kalamazoo, Michigan

Edited by Richard Brewer

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ILLUSTRATIONS

Illustrations not associated with specific papers are listed below. All are of plants, animals, or persons connected with Michigan prairies.

Cover and half-title page: Eastern meadowlark, *Sturnella magna,* on bur-oak, *Quercus macrocarpa.* Pen and ink by Barbara Jean King.

Page viii: Clarence R. Hanes. Photographer unknown.

Page 2: Prairie dock, *Silphium terebinthinaceum.* Photograph by Clayton D. Alway.

Page 21: Wild indigo, *Baptisia leucantha,* buds. Photograph by Clayton D. Alway.

Page 22: Turkey vulture, *Cathartes aura,* with side-oats grama, *Bouteloua curtipendula.* Pen and ink by Barbara Jean King.

Page 68: Prairie smoke, *Geum triflorum.* Pen and ink by Barbara Jean King.

Page 114: Wild indigo, *Baptisia leucantha,* flowers. Photograph by Clayton D. Alway.

Page 148: Wild indigo, *Baptisia leucantha,* seed pods. Photograph by Clayton D. Alway.

Page 163: Prairie coneflower, *Ratibida pinnata.* Photograph by Richard Brewer.

Page 176: Leslie A. Kenoyer. Photographer unknown.

Back cover: Prairie violet, *Viola pedatifida.* Pen and ink by Harvey E. Ballard, Jr.

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PART 5. USE OF PRAIRIE AND PRAIRIE PLANTS

PREFACE

It is fair to date the beginning of scientific study of prairie in Michigan from 1917, although there are perceptive comments in earlier, primarily floristic, accounts. In 1917, Henry A. Gleason, an Illinoisan well acquainted with native grassland, published *A Prairie Near Ann Arbor, Michigan* (Rhodora 19:163-165). Other vegetation types were more popular subjects for early study, however, and by 1950 entries in the scientific canon for Michigan grassland still numbered fewer than ten. Some noteworthy members were articles by Clarence R. Hanes (page viii), Leslie A. Kenoyer (page 176), and Jethro Otto Veatch. Non-scientific or historical writings were more numerous. Probably the best known work in this category is James Fenimore Cooper's 1848 novel *The Oak Openings* which is set in and around Prairie Ronde in Kalamazoo County.

Between 1950 and 1982, the year of the Eighth North American Prairie Conference, held in Kalamazoo, scientific studies of prairie multiplied. One factor facilitating this increase was a historical contribution, a long article by Albert F. Butler published in parts between 1947 and 1949. Its 60-odd pages of prairie lore, along with the early scientific studies mentioned, have been useful guides for the students of the past thirty years. The prologue to this volume is a reminiscence by Butler about the days when he was preparing his prairie sketches.

Represented in this volume either as full-length articles or by abstract are all the papers given at formal sessions of the Eighth North American Prairie Conference. No attempt was made to include presentations from workshops or interpretive sessions, although manuscripts from a few of the latter were submitted and are included. Each paper was reviewed by one or more persons outside the editorial staff. Reviewers are listed opposite the title page. I am grateful for their careful, fast work and also grateful to the authors who, with only a few exceptions, provided prompt, responsive revisions, even though these often required substantial condensation.

The subdivisions of this book do not correspond precisely with the original sessions of the conference. It is probably unnecessary to note that many papers would fit well into one or more sections besides the one where they were placed.

Harvey E. Ballard, Jr., Lucy S. Brewer, and Christy Fox served as assistant editors. They put in many hours per week over a ten-month period. I thank them. It is a simple statement of fact that without their efforts, the editing could not have been completed.

Plant nomenclature was a minor editorial problem. In the instructions to authors, we requested that they follow Gleason and Cronquist's *Manual* or, else, state and follow some alternative nomenclatural source. The degree to which manuscripts adhered to this request varied remarkably. Especially noteworthy was the lack of connection between stating a nomenclatural source and following it. Most of the papers published here follow Gleason and Cronquist (*Andropogon gerardi* is corrected to *A. gerardii* and specific epithets are not capitalized). Where another source is stated, the paper follows that source insofar as we were able to persuade the author to do what he or she claimed, without wasting too much of our time on it.

Common names generally follow Gleason and Cronquist or Courtenay and Zimmerman's *Wildflowers and Weeds* (1972, Van Nostrand Reinhold, New York). In this case, also, if an author had developed an unusual fondness for some particular name, we generally retained it.

One conclusion I have drawn is that adherence to a periodically revised checklist of North American plants for publication purposes would save authors, editors, and readers time. By focusing attention on situations where differences of opinion exist, it would also, in the long run, aid progress in plant systematics. At least on an interim basis, Kartesz and Kartesz (1980. *A Synonymized Checklist of the Vascular Flora of the United States, Canada, and Greenland.* Univ. North Carolina Press, Chapel Hill) would serve admirably, although standardized common names would also be useful.

The fire-grass-oak logo used during the conference and continued here was a joint product of Pam Rups, Kim Chapman, and Elizabeth Longhurst.

The drawings and photographs of Michigan plants and animals (page iv) add considerably to the attractiveness of the volume. For use of their work, I am indebted to Clayton Alway, who has helped me in similar fashion on another occasion; to Harvey Ballard for the pen and ink drawing of a priarie representative of one of his favorite groups; and to Barbara Jean King whose pen and ink drawings add grace to all the pages where they occur. The photographs of Clarence Hanes and Leslie Kenoyer were made available by Richard Pippen and Harriette Bartoo.

The work of the members of the Committee on Arrangements should be acknowledged. It is impractical to list everyone, although all performed essential functions; I should, nevertheless, mention Peg Kohring, general coordinator; Richard Pippen, program chairperson and seeker of funds for publication, and Kim Chapman, field trip coordinator (among many other services including poetry contest chairman).

The helpfulness and patience of WMU's Printing Services staff contributed greatly to the preparation of this volume.

Two presentations from the Conference have been published elsewhere. *Description, Distribution, and Ecology of Helianthus rota-plasticus, new species,* written by Charles C. King, Joyce Powers, and Michelle Powers and delivered as one of the highlights of the banquet by Dr. King was published in *Prairie/Plains Journal* no. 4 (fall) 1982, pages 40-42, and also in *Missouriensis,* vol. 4, 1982, pages 44-45. One of the winning entries in the poetry contest, *Moving West* by Don Stap was published in *Prairie/Plains Journal* no. 4 (fall) 1982, page 19.

Support for the editing and publishing of this volume came from several sources. A grant from the Audubon Society of Kalamazoo helped defray certain editorial expenses. Western Michigan University provided facilities and support for Brewer. The finishing touches to the volume during September 1983 came during the tenure of a sabbatical. Several authors or their institutions helped to defray page costs. A gift from the Western Michigan University Development Fund provided the capstone.

13 September 1983
Kalamazoo, Michigan

Clarence R. Hanes, about 1933. Photographer unknown. Hanes and his wife, Florence N. Hanes, lived in Schoolcraft, Michigan, in the middle of what was once the largest prairie in the state, Prairie Ronde. They began serious botanizing in the early 1930s, the heart of the Great Depression, partly as a way of concentrating on something other than the bleakness of the times. At first walking and bicycling were their only means of transportation but in 1933 they were able to buy a second-hand truck and it became feasible to cover the whole county intensively. The *Flora of Kalamazoo County, Michigan* (1947, privately published, Schoolcraft, Michigan) and *Cooper's Island from a Botanist's Viewpoint* (Michigan History 28:415-419, 1944) are important sources of information about the prairie region of Michigan.

PROLOGUE: REMEMBERING MICHIGAN'S PRAIRIES

ALBERT F. BUTLER

Two of the volumes of Carl Sandburg's biography of Lincoln are called *The Prairie Years.* As a young man Lincoln lived near Goosenest Prairie in Illinois. He read *The Prairie Beacon,* a newspaper published in nearby Paris, Illinois.

Included in Sandburg's volume *Cornhuskers* is the colorful poem titled "Prairie" which begins

> I was born on the prairie and the milk of its wheat, the red of its clover, the eyes of its women, gave me a song and a slogan.[1]

Since my youthful days I have admired Lincoln, and Sandburg, and prairies. I of course never saw Lincoln, nor did Sandburg, but both men spent much of their lives in Illinois, one of the greatest of the prairie states. And both men were in Michigan: Lincoln, in Kalamazoo for a political speech in 1856, and Sandburg, at Harbert where he lived for a time on the shore of Lake Michigan in Berrien County.

Michigan is not one of the great prairie regions but it is delightfully punctuated by numerous prairies clustered mostly in the southwestern corner of the state. The vast prairies of the West with ruler-straight horizons stretching for miles are not here. Michigan may not be one of the greatest prairie states but it is nevertheless a unique prairie state.

It would be hard to be a prairie searcher without traveling. It's no armchair job. When I was a young man I had a traveling position with a textbook publisher. I called at schools and colleges in Michigan. My work took me to nearly every Michigan city and town, large and small.

I did my regular work faithfully, but also carried on some prairie searching and researching "on the side." My expense account never mentioned prairie expenses, but there was a slight prairie flavor mixed with the daily facts and figures. The prairie scent was there however faint.

My prairie count eventually approached three score, with 58 actual sites finally located. The greatest prairie concentration I found to be in five counties: Kalamazoo, Calhoun, Cass, St. Joseph, and Branch. I drove about these areas, tramped across the prairies, interviewed local residents, newsmen, and librarians. Biology teachers in high schools were sometimes helpful with information on shrubs, plants, and prairie locations.

Of all the newspeople I met I hold in highest esteem and fond memory Mr. Charles A. Weissert, state editor of the *Kalamazoo Gazette.* He knew the state like the back of his hand. He knew much about prairies. We had good times discussing them.

Weissert presented me with a set of unbound pages of his book, *Southwestern Michigan* which is a storehouse of prairie information. The book appears as Volume III of the series, *Historic Michigan.* My unbound pages were soon bound and identified by an attractive backstrip, also a gift from the author.

I shall always remember this gentleman. He was a Harvard alumnus with stories to tell about memorable professors such as George Lyman Kittredge and Bliss Perry.

Overnight stops at such cities as Kalamazoo, Battle Creek, Benton Harbor, St. Joseph, Niles, Sturgis, and Coldwater—to name only a few—gave me available hours to spend in libraries with helpful librarians and local history materials. There is no better place to discover the rich lore of the prairies than each of the prairie neighborhoods.

A typical example is Prairie Ronde just south of Kalamazoo where I found Clarence and Florence Hanes at Schoolcraft with their enclosed front porch full of prairie plants and shrubs. Clarence guided me about Prairie Ronde and the Big Island; he gave me the best possible kind of prairie tour including a stop at the Abram Shaver memorial commemorating this pioneer ploughman never to be forgotten. I saw manuscript pages, too, of the Hanes' book *Flora of Kalamazoo County* published in 1947. My inscribed copy is well-worn and marked up with my notes and underscorings.

Fortuitous happenings were in my favor at times. One morning I stopped at New Troy in Berrien County to see my friend, Ed Eccles, the school superintendent (I had been checking on nearby Wolf Prairie); Ed said, "How would you like to meet one of Carl Sandburg's daughters?" Of course I was delighted to greet this personable girl who was a student in the New Troy High School. She and I had a good talk about her father and his great writing career. The Sandburg home was just beyond the shoulder of a great dune on the shore of Lake Michigan.

Still another unusual event was my call at the office of the Kalamazoo Public Library to get permission to copy the three illustrations that appear on page 127 of *Michigan History* for June, 1949; these are the pictures used in my piece on the Michigan prairies. I was given permission to borrow the large volume with the pictures provided that one of their employees—a young man—accompany me with the book while we walked over to a photographic establishment. The young man was well informed on prairies and we had a fine visit about prairie research and writing. Wherever he is now, I hope he will see this paragraph. And, yes, he returned the great book to the Kalamazoo Public Library.

As I think back on the pulse of life on Michigan's prairies, I am thankful that I did the fifty-eight brief sketches[2] when I did. Since then changes have come about that make some of those choice spots hard to find and identify. Some exist now only in memory.

It is said that the population of this country will continue to increase year-by-year until the year 2100. By then the census count may total 350 million. And by that time prairie memories will be more precious than ever. We should do everything possible to preserve them.

—5260 Woodcrest Drive, Minneapolis, Minnesota 55424

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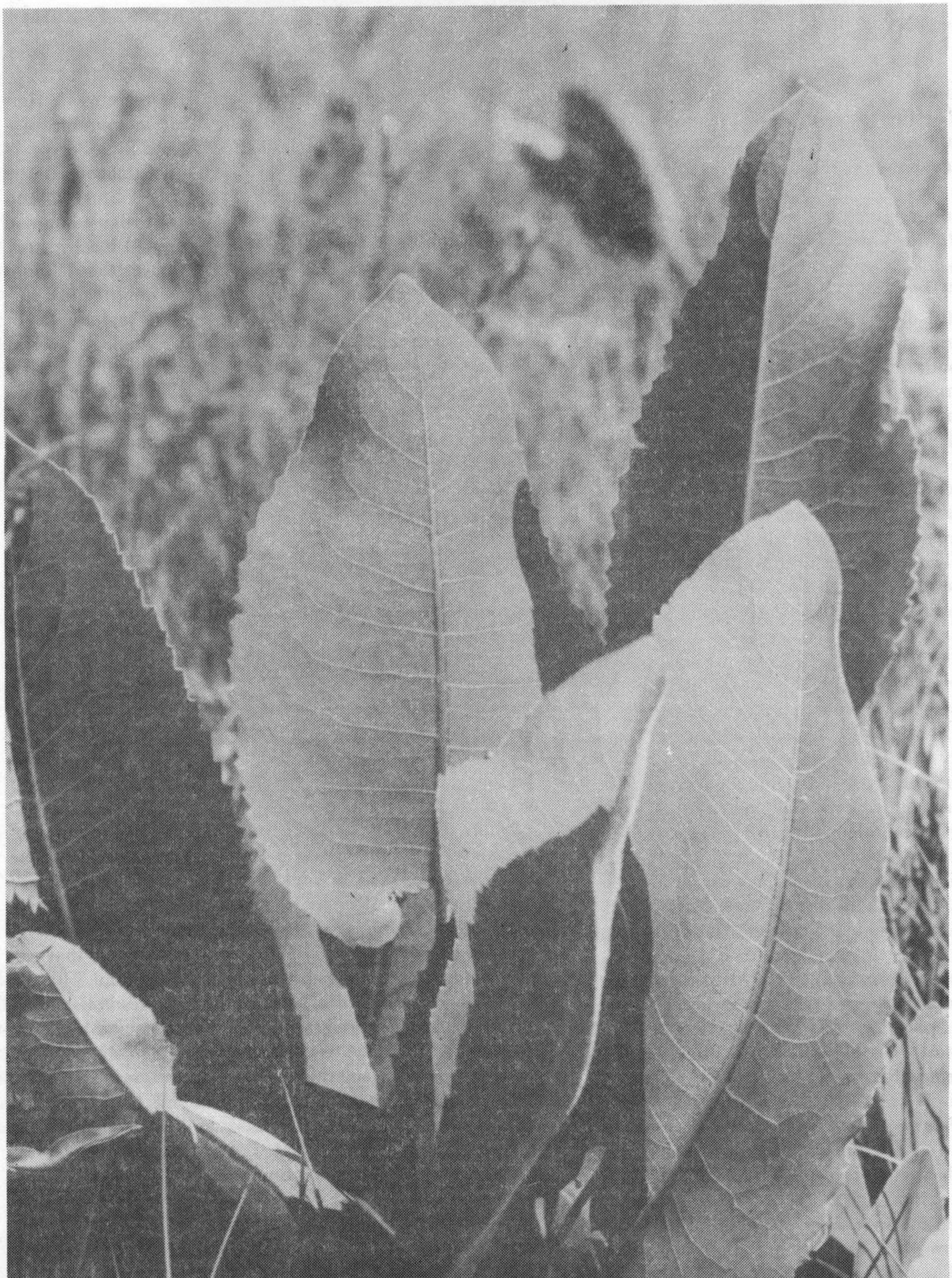
[1] From "Prairie" in *Cornhuskers,* copyright 1918 by Holt, Rinehart and Winston, Inc.; renewed 1946 by Carl Sandburg. Reprinted by permission of Harcourt Brace Jovanovich.

[2] Those interested in reading the sketches will find them in *Michigan History* for September 1947, March 1948, June 1949, and September 1949. They appear under the general title of *Rediscovering Michigan's Prairies.*

Part 1. Physical Factors and Autecology



NUMBER OF SEEDLINGS ESTABLISHED FROM STORED PRAIRIE HAY

R. E. Ries and L. Hofmann

USDA-ARS, P. O. Box 459, Mandan, North Dakota 58554

Abstract. Hay harvested from natural grasslands has been used as a seed source for revegetating disturbed areas. The harvested hay is mulched over the area to be revegetated and anchored by disking. Seeds contained in the hay then germinate and establish a new plant community.

A study was conducted to evaluate the effect of storage time on seeds present in prairie hay. Prairie hay was harvested from rangeland during the 1978 growing season and was mulched and germinated over steam heat-treated soil in flats in the greenhouse during the winter of 1978-79 (nonstored). A portion of this same hay was stored in an unheated building for 1 year and was then mulched and germinated, as before, during the winter of 1979-80 (stored). The number of established seedlings was compared from the nonstored and stored prairie hay.

The number of established seedlings of four species, prairie Junegrass (*Koeleria cristata*), threadleaf sedge (*Carex filifolia*), fringed sage (*Artemisia frigida*) and yellow whitlowwort (*Draba nemorosa*) increased significantly ($P < .05$) after the hay was stored for one year. Storage had no significant effect on number of established seedlings for all other species when comparing the nonstored and stored hay. Three other species (known to be present in the 1978 harvested hay) established for the first time from the stored hay. In this study, 1 year of storage did not reduce the number of established seedlings from prairie hay used as a seed source.

INTRODUCTION

Native hay was used as a source of seeds for re-establishing grasses in the Central Great Plains after the drought years of the 1930s. Wenger (1941) described techniques for using hay to establish grass on rough, erosive, and unproductive cropland, and listed the following advantages of the hay method: (1) there is no cash outlay for seeds; (2) a natural mixture of adapted native grasses is obtained; (3) the hay mulch provides protection from both wind and water erosion for the tender young seedlings while they are becoming established; (4) no special native grass seed processing or drilling equipment is necessary; and (5) better stands and fewer failures have resulted with the hay method than with drill seeding.

Very few reports on the use of the hay method for plant establishment have been published since the early 1940s. However, Gates (1962) and Eck et al. (1968) used the technique successfully to revegetate harsh sites in northern Idaho and in the Southern Great Plains, respectively.

In the late 1960s, increased surface-mining for coal in the Northern Great Plains increased the disturbance of native grasslands and rekindled an interest in the hay method to re-establish native vegetation on these disturbed areas. In an attempt to re-establish a native community, Whitman (1977) seeded annual species to speed secondary succession and then, 1 year later, he mulched late-cut prairie hay over the stubble of the annual species and anchored it by disking. The author concluded that the prairie hay contained enough viable seed to produce a community similar to the native community prior to mining. Prairie Junegrass was the most abundant perennial species initially established. Ries (1978) evaluated the effect of 5 harvest dates on seeds available from prairie hay and found that the kind and amount of seeds varied with harvest date and that at certain times excessive amounts of seed of any 1 species can be present, which may be undesirable. Another study (Ries et al. 1980) evaluated whether range condition (the current productivity of a range relative to its natural capability) was also related to the kind and amount of seeds found in prairie hay. They found that harvest date and range condition governed the kind and amount of potential seedlings contained in prairie hay and that the amount of seeds contained in prairie hay can be considerable. The authors concluded that the use of prairie hay as a seed

TABLE 1. Number of seedlings observed establishing from nonstored and stored prairie hay (seedlings per kg of hay).

Species[1]	Common Name	Nonstored Hay	Stored Hay
Perennial Grasses			
Bouteloua gracilis	blue grama	5a[2]	4a
Carex filifolia	threadleaf sedge	0b	2a
Koeleria cristata	prairie Junegrass	743b	1204a
Poa pratensis	Ken. bluegrass	142a	124a
Stipa comata	needle-and-thread	18a	18a
Stipa viridula	green needlegrass	7a	5a
Perennial Forbs			
Lotus corniculatus	birdsfoot trefoil	0a	1a
Petalostemum purpureum	purple prairie-clover	0a	4a
Potentilla pensylvanica	cinquefoil	35a	5a
Oxytropis lambertii	Lambert crazyweed	0a	1a
Ratibida columnifera	prairie coneflower	71a	35a
Solidago missouriensis	Missouri goldenrod	53a	71a
Taraxacum officinale	dandelion	18a	18a
Shrub			
Artemisia frigida	fringed sage	35b	124a
Annual Grass			
Festuca octoflora	sixweeks fescue	142a	142a
Annual and Biennial Forbs			
Androsace occidentalis	fairy candelabra	18a	35a
Draba nemorosa	yellow whitlowwort	4b	18a
Hedeoma hispida	false pennyroyal	566a	779a
Lepidium densiflorum	pepperweed	35a	53a
Linum rigidum	stiffstem flax	53a	53a

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[1] Names according to Stevens (1963).

[2] Average values in rows with different letters differ significantly at the 5% level of probability, according to Duncan's multiple range test.

TABLE 2. Number of seedlings observed establishing from prairie hay harvested in different years (seedlings per kg of hay)

SPECIES[1]	COMMON NAME	1978	1980	1981
Perennial Grasses				
Bouteloua gracilis	blue grama	4b[2]	1735a	88b
Carex filifolia	threadleaf sedge	—[3]	—	—
Koeleria cristata	prairie Junegrass	7062b	18b	45,436a
Poa pratensis	Kentucky bluegrass	1487a	0b	18b
Stipa comata	needle-and-thread	177b	18b	513a
Stipa viridula	green needlegrass	53b	0b	319a
Perennial Forbs				
Lotus corniculatus	birdsfoot trefoil	—[3]	—	—
Petalostemum purpureum	purple prairie-clover	0a	0a	9a
Potentilla pensylvanica	cinquefoil	177a	0a	159a
Oxytropis lambertii	Lambert crazyweed	—[3]	—	—
Ratibida columnifera	prairie coneflower	673a	0b	18b
Solidago missouriensis	Missouri goldenrod	354a	4b	9b
Taraxacum officinale	dandelion	124a	0b	53ab
Shrub				
Artemisia frigida	fringed sage	283a	35b	124ab
Annual Grass				
Festuca octoflora	sixweeks fescue	531a	0b	0b
Annual and Biennial Forbs				
Androsace occidentalis	fairy candelabra	106a	0a	0a
Draba nemorosa	yellow whitlowwort	4a	9a	4a
Hedeoma hispida	false pennyroyal	5239a	53b	35b
Lepidium densiflorum	pepperweed	177a	18b	18b
Linum rigidum	stiffstem flax	212a	0b	0b

[1] Names according to Stevens (1963).

[2] Average values in rows with different letters differ significantly at the 5% level of probability, according to Duncan's multiple range test.

[3] Not observed establishing from hay except after storage.

source appeared to be feasible for revegetating disturbed areas in parks and natural areas, for landscaping private and public lands, for revegetation of surface-mine land, and for range improvement.

The purpose of this paper is to report initial findings on the effect of storage time of prairie hay on the number of establishing seedlings.

STUDY AREA AND METHODS

The study area and methods used in the study of prairie hay were described in detail by Ries et al. (1980). The prairie hay was harvested at monthly intervals from June through October during the 1978, 1980, and 1981 growing seasons from rangeland in excellent, good, and fair condition on a silty range site near Mandan, North Dakota. The hay was air dried and mulched at a rate of 336 g/m² over steam heat-treated soil in flats in the greenhouse during the winter following harvest. Seedlings emerging from the soil were considered established and the number was counted by species and used as an index of the potential kind and amount of seedlings contained in the prairie hay obtained from different years, harvest dates, and range conditions.

A portion of prairie hay harvested during the 1978 growing season was used to study the effects of storage. The hay was stored in an unheated building (temperature ranged from −20 to 30°C) for 1 year. During the winter of 1979-80 the stored hay was germinated in the same manner as before.

Data obtained from germinating mulched nonstored and stored hay were analyzed to determine if 1 year of storage significantly affected the number of established seedlings. Data obtained from germinating nonstored hay harvested in 1978, 1980, and 1981 were subjected to analysis of variance to determine significant differences in the number of established seedlings among the 3 years studied.

RESULTS

The number of established seedlings of prairie Junegrass, threadleaf sedge, fringed sage and yellow whitlowwort increased significantly after 1 year of storage (Table 1). The number of established seedlings did not change significantly after one year of storage for all other species. Birdsfoot trefoil, purple prairie-clover and Lambert crazyweed became established from prairie hay only after the hay had been stored.

Numbers of observed seedlings in nonstored prairie hay harvested in different years are presented in Table 2. All species, except for purple prairie-clover, cinquefoil, fairy candelabra and yellow whitlowwort, were significantly different in number of established seedlings observed between years.

DISCUSSION

The number of seeds contained in prairie hay changed from year to year (Table 2). To obtain hay with the highest level of a desired species, hay will have to be harvested in a year favorable to seed production of that species. Since this does not occur every year, hay harvested from the good seed year will have to be stored. The length of time the hay can be stored without a significant decrease in viability of desired seeds therefore becomes important.

Results from this study on prairie hay storage are encouraging. Four species had significantly more seedlings established after storing the hay for 1 year than when the hay was germinated the winter immediately after harvest. Three species established seedlings for the first time after 1 year of storage. All other species had statistically the same number of established seedlings after 1 year of storage when compared with nonstored hay. Therefore, the germination potential for the seed of all species studied remained the same or increased after 1 year's storage. Seeds of seven species appear to have germinated better after one year of storage, perhaps due to the need for an after-ripening period.

Work is continuing to determine the maximum length of storage that can be used without reducing the number of seedlings yielded by the stored prairie hay.

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SOIL *p*H OF A TALLGRASS SAND PRAIRIE

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Abstract. Soil sampling lines were established in 3 distinct vegetational areas of the 40-ha Gensburg-Markham Prairie. This prairie is located on lacustrine deposits of glacial Lake Chicago in the Chicago Lake Plain physiographic region of Illinois.

A sampling line consisting of 10 sampling points, each 20 m apart, was established in an area of big bluestem-Indian grass, little bluestem-June grass, and cordgrass-bluejoint grass. Soil samples to be tested for *p*H were taken from depths of 15, 30, 45, and 60 cm. Sampling along each line was done in May, July, and October.

Results showed that the areas of big bluestem-Indian grass and little bluestem-June grass, both located on a Watseka loamy fine sand were acidic (*p*H 4.4-6.4). Generally, the subsoils were more acidic than the upper soil layers due to the underlying sand. The area of cordgrass-bluejoint grass, located on a Selma loam, was slightly acidic to slightly alkaline (*p*H 6.1-7.7). The upper soil layer was more acidic than the subsoil layer due to the presence of marl in the subsoil.

INTRODUCTION

The data and results discussed in this paper were compiled at the Gensburg-Markham Prairie during the 1979 field season (Post 1980). Interest in soil *p*H at this prairie was stimulated by field observation that certain plants grew only in specific parts of the prairie. Since little information exists in the literature concerning a correlation between soil *p*H and plant distribution it was decided to sample to determine if direct correlations could be observed.

METHODS

The study was done at the Gensburg-Markham Prairie, a 40-ha prairie located in Cook County, Illinois. The prairie is located on the Chicago lacustrine plain formed by the retreat of glacial Lake Chicago (Hanson 1975); as a result soils are varied. A low, sandy beach ridge runs from the southeast to the northwest paralleled by a lower swale area. Two low sand spits are found in the eastern third of the prairie (Fig. 1). The soils making up the beach ridge are Watseka loamy fine sand, Selma loam in the swale and Hoopeston fine sandy loam forming the sand spits (Mapes 1979).

Two sampling lines were established in the Watseka loamy fine sand soil type and 1 line was established in the Selma loam. Of the 2 lines in the Watseka soil type, 1 was in an area that had been plowed 60 years ago but was now vegetated primarily by prairie species such as big bluestem (*Andropogon gerardii*) and Indian grass (*Sorghastrum nutans*). The other line was in an area that as far as could be determined had never been plowed. The vegetation here was dominated by forbs and shrubs, including blueberry (*Vaccinium angustifolium*) and huckleberry (*Gaylussacia baccata*). Grasses were sparse and were either little bluestem (*Andropogon scoparius*) or June grass (*Koeleria cristata*) with some sedge (*Carex pensylvanica*) present.

The sampling line in the Selma loam type was established in an area characterized by cordgrass (*Spartina pectinata*), bluejoint grass (*Calamagrostis canadensis*) and sedge (*Carex stricta*).

Samples were taken in May, July, and October at depths of 15, 30, 45 and 60 cm (6, 12, 18, 24 inches) using a standard open-bore soil probe. They were placed in plastic vials and analyzed as quickly as possible in the laboratory, usually within 1-2 hours of collection. One g of soil was placed in 20 ml of distilled water and swirled at 0, 30, and 60 minutes. After swirling at 60 minutes the *p*H of this slurry was recorded with a Beckman pistol *p*H meter (U.S. Dept. of Agriculture Circular No. 757).

RESULTS

Results from sampling in an area of the old beach ridge that had previously been disturbed by plowing (Table 1) showed the area to be moderately acidic in the first 6 inches of soil, becoming more strongly acidic in the subsoil. As the growing season progressed, the first 6 inches became slightly more acidic; this change was not as noticeable in the subsoil layers. At sample points 1, 1a, and 1b the soil *p*H was determined to be remarkably calcareous to only slightly acidic regardless of the sampling time.

Line 2, located in an undisturbed portion of the prairie on the old beach ridge, had remarkably acidic soil. Again, a slight decline in *p*H in the top 6 inches of the soil can be seen during the course of the growing season (Table 2). Unlike soil line 1 the *p*H here appeared to be uniform over a large area.

Line 3, located in a swale or wet area, was neutral to slightly acid, becoming more alkaline in the subsoil layers. Again, the top 6 inches of soil showed an increase in acidity as the growing season progressed (Table 3).

DISCUSSION

Steiger (1930) recorded soil *p*H values for both an upland and lowland prairie. His upland prairie was composed of little bluestem and June grass. His values ranged from slightly acid in the topsoil to slightly alkaline in the subsoil as compared to values that were slightly acid in the topsoil to acid in the subsoil in this study. For lowland prairie of big bluestem and Indian grass he recorded almost neutral values as opposed to acid values determined in this study.

Bliss and Cox (1964) correlated *p*H values for different soil horizons with the prairie grasses found growing there.

TABLE 1. Soil *p*H for farmed beach ridge (Line 1).

	DEPTH (CM)			
DATE	15	30	45	60
May (14 samples)				
Median	6.3	5.75	6.75	6.5
Range	6.0-7.8	5.3-8.0	5.4-8.1	5.0-8.0
July (40 samples)				
Median	5.6	5.2	5.1	5.05
Range	5.3-8.5	4.7-8.6	4.7-8.2	4.6-8.3
October (44 samples)				
Median	5.5	5.2	5.0	4.9
Range	5.3-8.2	4.9-8.4	4.6-8.5	4.6-7.7

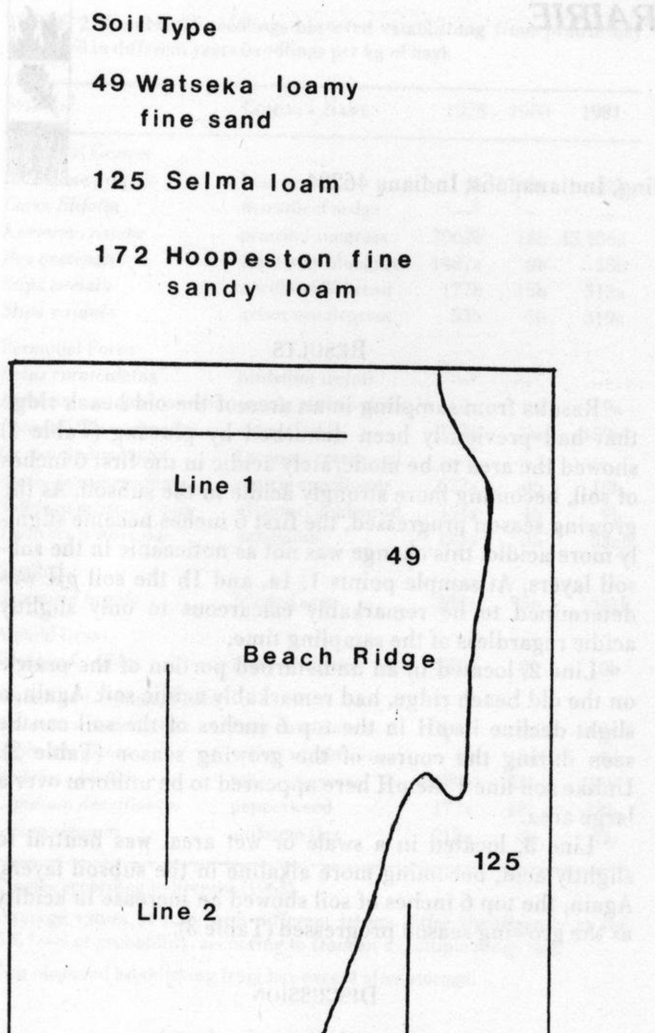

FIG. 1. Location of soil types, sampling lines and ridge and swale areas in the Gensburg-Markham Prairie.

TABLE 2. Soil *p*H for non-farmed beach ridge (Line 2).

	DEPTH (CM)			
DATE	15	30	45	60
May (16 samples)				
Median	5.3	4.6	4.4	4.5
Range	4.8-6.4	4.4-5.0	4.3-4.9	4.4-4.6
July (40 samples)				
Median	5.25	4.8	4.65	4.6
Range	4.9-5.6	4.6-5.8	4.5-5.0	4.4-5.0
October (40 samples)				
Median	4.8	4.65	4.6	4.5
Range	4.4-5.1	4.4-5.0	4.4-4.8	4.3-4.8

For areas of big and little bluestem they recorded values similar to those found in this study. A distinct difference was that they recorded slightly acidic values for an area of cordgrass whereas this study found neutral to slightly alkaline soil *p*H under this grass type.

Watseka loamy fine sand is black loamy sand at the surface and loamy fine and gray fine sand in the subsoil (Mapes 1979). Soil reaction is reported to range from strongly acid to slightly acid in the subsoil while soil reaction in the surface layer varies, depending on past management, but is commonly neutral or slightly acid. Data from line 1 is fairly consistent with this description except for 2 adjacent sampling points. Here the soil was distinctly alkaline at all soil depths. It appears that these sampling points were placed in an area where the soil showed more characteristics of the Selma loam than the Watseka fine loamy sand. The plants growing in the vicinity of these 2 sampling points also reflect the differences. Distinct calciphiles such as golden alexanders (*Zizea aurea*) and valerian (*Valeriana edulis* var. *ciliata*) grew in the vicinity here and nowhere else on the Watseka soil type. Along the rest of soil line 1 big bluestem, Indian grass, spike blazing star (*Liatris spicata*) and goldenrods (*Solidago* spp.) were common plants. Line 2 was also located on the Watseka soil type. Results from this area also approximated the description of this soil type. Soils tended to be more acidic here than anywhere else in the prairie, ranging from 4.4-5.0. Several plants were observed growing in this part of the prairie and nowhere else and included huckleberry and blueberry.

TABLE 3. Soil *p*H for swale area (Line 3).

	DEPTH (CM)			
DATE	15	30	45	60
May (12 samples)				
Median	6.75	6.55	6.6	(Too wet to
Range	6.2-6.9	6.4-6.7	6.5-6.7	sample)
July (40 samples)				
Median	6.6	6.9	7.1	7.3
Range	6.4-7.1	6.6-7.1	6.9-7.5	7.0-8.4
October (42 samples)				
Median	6.35	6.4	6.45	6.6
Range	6.1-6.8	6.1-6.5	6.3-6.7	6.2-6.8

A puzzling contrast was observed between lines 1 and 2. Both were located on the same Watseka loamy fine sand, but line 1 was much less acidic. The area where line 1 is located was disturbed by farming, as old plow lines can still be seen. Mixing of the soil resulting from cultivation may be the reason for the observed differences in soil pH. Line 2, located in an area where farming was not attempted, in all likelihood represents the original soil conditions of the prairie in the upland areas.

Line 3 differed greatly from the other 2 soil lines both in vegetation present and soil reaction. Soil here was classified as Selma loam with soil reaction neutral at the surface to alkaline in the subsoil (Mapes 1979). My results agree with this description.

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THE FLOWERING RESPONSES OF 7 GRASSES TO SEASONAL TIMING OF PRESCRIBED BURNS IN REMNANT WISCONSIN PRAIRIE

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Abstract. For 3 years burn treatments were applied in early spring, late spring, and late fall to 2 remnant Wisconsin prairie stands. The stands represented dry and dry-mesic prairie types. Permanent quadrats were sampled near the beginning and end of the growing seasons following the treatments.

The flowering responses of the dominant grasses tended to follow 1 of 2 patterns. Cool-season grasses such as *Poa* spp., *Panicum* spp., and *Bromus kalmii* were unaffected by early spring burns while late spring fires greatly reduced their flowering.

Sorghastrum nutans, *Andropogon scoparius*, *Andropogon gerardii*, and *Bouteloua curtipendula* generally had their flowering stimulated by all the burns with the most stimulus coming from late spring treatments.

INTRODUCTION

The objective of this study was to investigate 2 variables of prairie-fire ecology that may influence the response of prairie vegetation to fire: (1) seasonal timing of fire, and (2) prairie type (soil moisture regime).

Prairie managers often question the long-term response of prairie flora to frequent prescribed burning. Because the majority of prairie plants are long-lived perennials which tend to have relatively slow rates of population loss and recruitment, the time needed to document pop;ulation changes could well be 10 years or longer. However, we believe that some easily measured short-term responses such as flowering, seed production, or seasonal growth may be used to indicate long-term population or community composition changes.

This 5-year project (begun in 1979) was designed to monitor both long- and short-term plant responses. Permanent quadrats have been established and will continue to be studied for long-term results. Short-term responses are being monitored in terms of the flower production of 7 dominant grasses and of plant vigor and flower production for 15 selected forbs. This paper deals only with information concerning the flowering of the grasses as affected by seasonal timing of prescribed burns and prairie type (Lovell et al. 1983) gives information on the forbs.

METHODS

Two prairie remnants located in south-central Wisconsin were selected for side-by-side plot comparisons of 3 different burn treatments on 2 different prairie types. At each site a rectangular 800 m² stand was selected and tested for within-stand uniformity on the basis of soil moisture, soil depth to bedrock, slope angle and aspect, and plant species composition. For the tests each stand was divided into 5 equal subunits.

Data on soil moisture, soil depth, steepness of slope, and aspect were collected from sample points within each subunit and tested by an analysis of variance (ANOVA) of their sample means (Henderson 1981). No significant difference was found in comparisons of subunits within a stand; however, there were significant differences between stands for soil moisture ($p < .0001$) and soil depth ($p < .05$).

Plant species frequency data obtained from 20 0.25-m² quadrats per subunit were compared using a modified Sørensen's index of similarity (Curtis 1959, Mueller-Dombois and Ellenberg 1974). Index values between subunits within a stand ranged from 0.72 to 0.90 with a mean of 0.85, indicating high similarity. The index value between the stands was 0.41.

On the basis of these findings, we considered the stands (1) to be uniform and thus suitable for dividing into separate treatment plots, and (2) to be of 2 different prairie types. Stand I, which is on the south-facing slope, was characterized as dry (*sensu* Curtis 1959) and Stand II, on a north-facing slope, was characterized as dry-mesic.

Each stand was divided into 4 rectangular plots (3 burn treatments and 1 control) which were oriented directly up-slope and separated by 1-m buffer strips. The plots were 120 m² in area at Stand 1 and 70 m² at Stand II. The prescribed burns were conducted in late fall (early December), early spring (late March to early April), and late spring (mid-May). Unfortunately fall burns were accomplished only on the dry site (Stand I). The burn treatments began in 1979-80 and were repeated annually on the same plots for 3 years. They were timed to phenology and not calendar date.

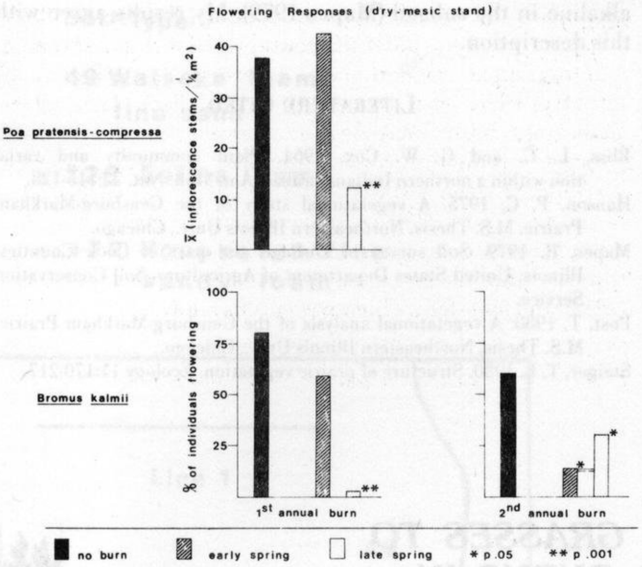

FIG. 1. Flowering responses of *Poa pratensis-compressa* and *Bromus kalmii.* Responses which are significantly different from the control are indicated by asterisks. Treatment responses connected by double bars are not significantly different at the $P = 0.05$ level.

Twenty 0.25 m² permanent quadrats were established in each test plot in a stratified random pattern. Following the treatments they were sampled twice during the growing season. Sod-forming grasses were checked as present, while the number of clumps was noted for bunch-forming species. The number of inflorescence stems per quadrat for sod-forming grasses and the number of inflorescence stems per individual or the percentage of individuals flowering for bunch grasses were noted. Data from 2 growing seasons (3, for *Panicum* spp.) are presented here.

RESULTS AND DISCUSSION

The cool-season species as a group exhibited 1 response pattern and the warm-season species another (Figs. 1-3). Cool-season grasses are those species which are active in early spring, become nearly dormant by mid-summer and become active again in autumn (Risser et al. 1981). They generally follow the C_3 photosynthetic pathway. Three species exhibiting this growth pattern are *Bromus kalmii* (prairie brome) in the dry-mesic stand, *Panicum leibergii-oligosanthes* (panic grass complex) in the dry stand, and *Poa pratensis-compressa* (blue grass complex) in the dry-mesic stand (Waller and Lewis 1979). Warm-season grasses are C_4 species which start development later in the year, reach a peak of activity in mid to late summer, and become dormant in early autumn (Risser et al. 1981). *Andropogon gerardii* (big bluestem), *Andropogon scoparius* (little bluestem), *Bouteloua curtipendula* (side-oats grama) and *Sorghastrum nutans* (Indian grass) follow this pattern (Waller and Lewis 1979).

The flowering of the cool-season grasses (Figs. 1, 2) was generally unaffected by the early spring burns. A notable exception was *Bromus kalmii.* In the second year the early spring burn resulted in a marked decrease in the number of *Bromus* individuals flowering. The response to the late spring burns was very pronounced and consistent. All 3 taxa had their flowering reduced by at least 70% in all years (Figs. 1, 2).

The flowering response of *Poa* to fire has been documented elsewhere. On a restored mesic prairie in Wisconsin Curtis and Partch (1948) obtained results that are nearly identical with those of this study. They found a March burn had no affect on the number of inflorescence stalks produced by *Poa* while a May burn decreased production by 80%. In contrast, Ehrenreich and Aikman (1963) on a mesic site in northeast Iowa found that early spring fires nearly eliminated *Poa* flowering. At the other extreme Zedler and Loucks (1969) reported an increase of inflorescences after early spring burns of 450% in a moist depression and no change on drier sandy ridges. It may be significant that the Zedler and Loucks study was conducted on nearly pure stands of *Poa* while the others dealt with bluegrass in diverse prairie communities where interspecific competition may have influenced the response.

The reason for the marked reduction in flowering of cool-season grasses following the late spring burn is not known. It may be the result of a reduction in carbohydrate reserves suffered as the season's new growth was killed by the fire. Not only would additional energy be lost in regrowth; it is likely that during regrowth the grasses would also be deprived of normal carbohydrate income in the middle of May, a high productivity period (Sosebee 1977, Stuckey 1941, Brown 1943).

The warm-season grasses generally showed an increase in flowering as a result of all 3 burn treatments, with the late spring burns providing a significantly greater stimulus (Figs. 3 and 4). This was especially true on the dry-mesic stand where the response to fire was consistently more dramatic than on the dry stand.

It is well known that fire generally stimulates the flowering of warm-season prairie grasses (Daubenmire 1968, Vogl 1974); how this occurs is not well documented. The general assumption in the literature is that the increase in flowering is a response to improved growing conditions, resulting from mulch removal that permits warm-season plants to begin growth early and to build up a favorable carbohydrate reserve before the normal period of flower primordium initiation (Curtis and Partch 1950, Ehrenreich and Aikman 1963, Old 1969, Hulbert 1969). Peet et al.

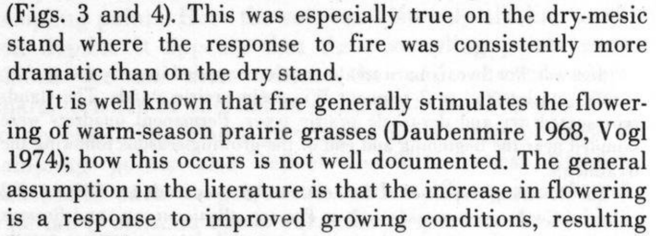

FIG. 2. Flowering response and total population of *Panicum leibergii-oligosanthes.* Population means are represented by dots. The bars represent 1 standard deviation.

(1975) documented that higher net photosynthate production occurs in *Andropogon gerardii* as a result of spring burning. Whether or not the increase in carbohydrate supplies is the cause of the increase in flowering has not yet been clearly documented for perennial prairie grasses. However, based on what is known about carbohydrate allocation, distribution, and translocation in grasses it is not unreasonable to assume that carbohydrate production early in the season plays a role in determining flower production later in the season (Moser 1977). Inflorescence and seed development are very strong carbohydrate sinks and it is known that carbohydrate reserves in grasses are drawn upon heavily by flower stalk production (Weinmann 1952).

Because of the potential causal relationship between net photosynthate production and inflorescence production and the fact that increases in flowering have been clearly associated with increases in above- and below-ground biomass production (Curtis and Partch 1948, Ehrenreich and Aikman 1963, Hadley and Kiekhefer 1963, Old 1969, Hill and Platt 1975) we believe that flowering may be a useful indicator of vigor and thus of long-term competitive ability within the community. To field test this hypothesis is one of the long-term objectives of this study.

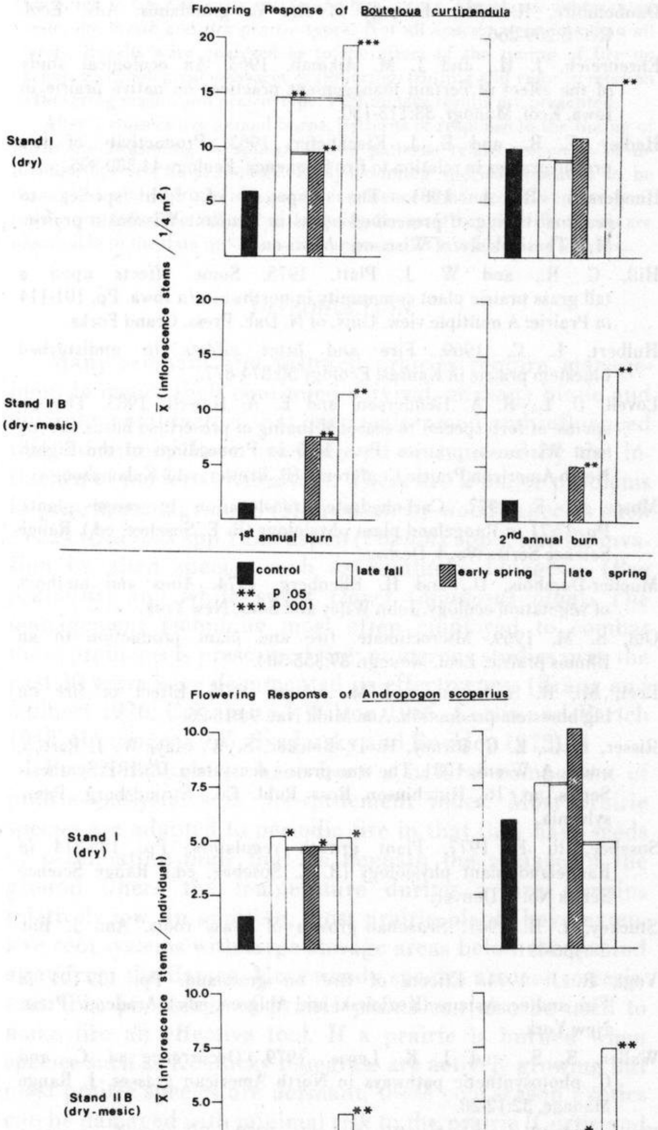

FIG. 3. Flowering responses of *Bouteloua curtipendula* and *Andropogon scoparius*. Responses which are significantly different from the control are indicated by asterisks. Treatment responses connected by double bars are not significantly different at the $P = 0.05$ level.

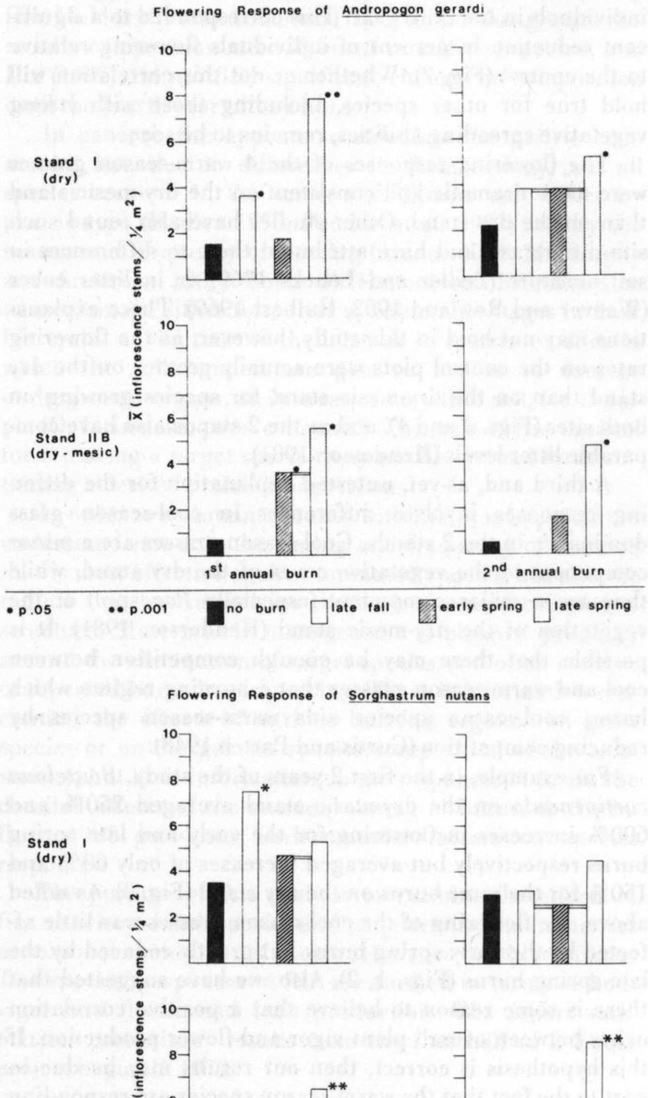

FIG. 4. Flowering responses of *Andropogon gerardii* and *Sorghastrum nutans*. Responses which are significantly different from the control are indicated by asterisks. Treatment responses connected by double bars are not significantly different at the $P = 0.05$ level.

One preliminary set of data which suggests a correlation between initial flowering response and population changes concerns the *Panicum leibergii-oligosanthes* group. Our experience suggests that this species complex contains long-lived individuals with little vegetative spreading ability. The total population remained relatively constant in the control, late fall, and early spring plots over a 3-year period (Fig. 2). The population means ranged from 2.5 to 3.5 individuals per 0.25 m^2. At the same time, the percentage of individuals flowering also showed little change between plots and over time. In the late spring burn plot, however, a significant population decline was observed from an initial average of 2.7 individuals per 0.25 m^2 to an average of 0.7 individuals in the third year. This corresponded to a significant reduction in percent of individuals flowering relative to the control (Fig. 2). Whether or not this correlation will hold true for other species, including those with strong vegetative spreading abilities, remains to be seen.

The flowering responses of the 4 warm-season grasses were more dramatic and consistent on the dry-mesic stand than on the dry stand. Other studies have also found such site differences and have attributed them to differences in soil moisture (Zedler and Loucks 1969) or in litter cover (Weaver and Rowland 1952, Hulbert 1969). These explanations may not hold in this study, however, as the flowering rates on the control plots were actually greater on the dry stand than on the dry-mesic stand for species growing on both sites (Figs. 3 and 4), and as the 2 stands also have comparable litter levels (Henderson 1981).

A third and, as-yet, untested explanation for the differing responses involves differences in cool-season grass dominance in the 2 stands. Cool-season grasses are a minor component of the vegetative cover of the dry stand, while they are a major component (especially *Poa* spp.) of the vegetation of the dry-mesic stand (Henderson 1981). It is possible that there may be enough competition between cool and warm-season grasses that a burning regime which harms cool-season species aids warm-season species by reducing competition (Curtis and Partch 1948).

For example, in the first 2 years of the study, *Bouteloua curtipendula* on the dry-mesic stand averaged 250% and 600% increases in flowering for the early and late spring burns respectively but averaged increases of only 60% and 150% for the same burns on the dry stand (Fig. 3). As noted above, the flowering of the cool-season grasses was little affected by the early spring burns but greatly reduced by the late spring burns (Figs. 1, 2). Also, we have suggested that there is some reason to believe that a positive correlation exists between overall plant vigor and flower production. If this hypothesis is correct, then our results may be due in part to the fact that the warm-season species are responding to a decrease in competition from cool-season grasses on the dry-mesic site. Again, this explanation needs further substantiation.

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THE RESPONSE OF FORB SPECIES TO SEASONAL TIMING OF PRESCRIBED BURNS IN REMNANT WISCONSIN PRAIRIES

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Abstract. The responses of 14 prairie forbs to prescribed burns were monitored on 3 remnant prairie stands in southern Wisconsin. Burns were conducted in late fall, early spring and late spring. The stands represented mesic, dry-mesic and dry prairie types. Not all species were found in all stands. Results were analyzed as to the effect of the timing of fire on various morphological measures of flowering, fruiting and vigor in relation to flowering season and prairie type. Preliminary results are presented.

After 2 consecutive annual burns, patterns of response to the timing of burns are beginning to appear. These patterns relate responses of individual species to phenology. Early-blooming species appeared to be damaged by late spring fires but to experience enhanced flower and fruit production following fall and early-spring burns. Other possible trends are observable in the data involving midsummer- and late-blooming species.

INTRODUCTION

Many remnant and restored prairies require management to insure their continued survival, as many biotic and environmental factors that once maintained and influenced this community have been altered or removed by the influence of modern civilization. There are 2 major problems in prairie management: (1) invasion by woody species such as oak (*Quercus* spp.) and aspen (*Populus* spp.), and (2) invasion by alien species such as Kentucky bluegrass (*Poa pratensis*) and white sweet clover (*Melilotus alba*). The management technique most often employed to combat these problems is prescribed fire; numerous studies over the past 30 years have documented its effectiveness (Bragg and Hulbert 1976, Cottam and Wilson 1966, Curtis and Partch 1948, Heitlinger 1975, Svedarsky and Buckley 1975).

Fire is thought to have been a natural component of prairie ecosystems in pre-settlement times. Most prairie species are adapted to periodic fire in that they have seeds or perennating buds that lie beneath the surface of the ground where the temperature during a fire remains relatively low. In addition, most prairie plants have extensive root systems with large storage areas below the ground away from the flames. Most woody species are not so resistant. The phenology of prairie plants can also be used to make fire an effective tool. If a prairie is burned when species such as Kentucky bluegrass are actively growing but most prairie species are dormant, these cool-season exotics can be damaged with minimal risk to the prairie (Curtis and Partch 1948, Ehrenreich and Aikman 1963).

In addition to damaging unwanted species, fire is known to affect the growth, flower production, and community structure of the prairie (Daubenmire 1968, Hill and Platt 1975). Old (1969) reported increases in growth and flowering of several native grasses following fire in Illinois, and Kucera and Ehrenreich (1962) obtained similar results in Missouri. Hulbert (1969) reported increased tiller production of *Andropogon gerardii* following burns in Kansas prairie. Ehrenreich and Aikman (1963) found that increases in flower production may persist for several years following fire. McMurphy and Anderson (1965) found changes in community composition after 30 burns in a 36-year period, and Dix (1960) did not find significant changes in composition until the fourth year after a burn.

In general, fire appears to stimulate the prairie community but, due to differences in their ecology, not all species respond in the same way. Effects may differ by prairie type (Hadley 1970, Pemble et al. 1981) and by the season and frequency of burning (Aldous 1934, McMurphy and Anderson 1965). Some differences can be related to tissue damage either to species at vulnerable stages in their life cycles at the time of the burn or to species on sites in which the soil temperature gets so hot as to damage underground organs, as in areas of very thin soil, for example (O. L. Loucks, pers. commun.). The type of fire optimal for removing a target species may not be optimal for maintaining a desired prairie composition.

In order to maintain a prairie with fire, it is important to understand not only the timing and frequency of burning that is most effective against unwanted species, but also the regime that best maintains the desired native community structure. Most prairie management is planned primarily around the elimination of target species and often consists of repeated burns in early spring. There is information concerning the effects of various burning regimes on grass species or on the general species composition of the community, but little information on the responses of forbs, the detailed effects of the seasonal timing of burns, or the influence of post-burn environmental factors on species responses.

The purpose of this study is to examine the effects of fire on selected forb species and to determine the influences of seasonal timing and site characteristics on these effects. The species' responses to fire are studied in terms of both vigor and flower and fruit production. The report summarizes preliminary results from the first half of a 5-year project begun in 1979.

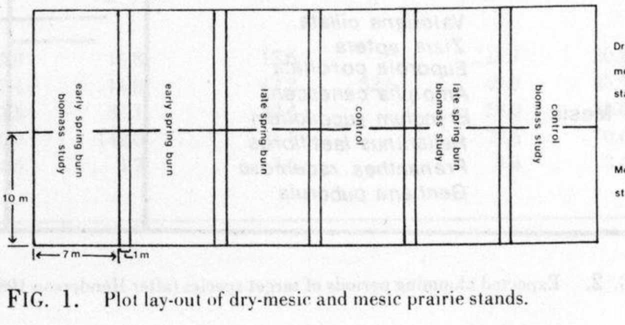

FIG. 1. Plot lay-out of dry-mesic and mesic prairie stands.

METHODS

Study Sites and Treatments

The 2 study sites, both on privately owned land in south-central Wisconsin, contain remnants of native prairie with high diversity and minimal disturbance. Site I is a dry prairie (*sensu* Curtis 1959) located on a south-facing slope. Site II includes 2 stands, a dry-mesic and a mesic prairie, both on a steep north-facing slope. Baseline data were collected on vegetation, soil depth and moisture, slope, and aspect. The vegetation data were analyzed with a modification of Sørensen's index of similarity (Curtis 1959, Mueller-Dombois and Ellenberg 1974), and the data on soil depth and moisture, slope and aspect were tested with ANOVA. On the basis of these tests, each stand was found to be sufficiently homogeneous to allow us to conclude that differences between treatments within a stand are due to the treatments and not to random fluctuations within the stand.

Burn treatments were those most commonly used by prairie managers. A fall burn simulates wildfires set by lightning or Indians prior to European settlement of the prairies. Our fall burn was done in the first week of December. An early spring burn (in late March or early April, at about the time that *Anemone patens* is coming into bloom) was timed to occur before most species break dormancy; such burns are used by prairie managers to control woody invasion and stimulate prairie growth. A late spring burn (in mid-May, at about the time that *Dodecatheon meadia* is coming into bloom) was applied when cool-season species are growing vigorously but warm-season species are not; such burns are commonly used to control invasion by herbaceous aliens and woody species. Each burn treatment was applied to a single plot in each of the stands, with the exception of the fall burn treatment which was applied only at Site I. Each stand also includes an unburned control plot (Fig. 1). Burn treatments were first applied in the fall of 1979 and the spring of 1980, and repeated the following year.

Forb Measurements

Fourteen species, representing a cross-section of common prairie forbs, were selected for study. Nine families are included and expected blooming periods range from May through October (Fig. 2). A variety of growth patterns are represented.

The traits measured, of necessity, vary with the morphology of the species, but were designed to provide estimates of vigor and reproductive response. Vigor estimates were generally made by counting growing points, leaves and/or stems and measuring the lengths of leaves and/or stems. Reproductive response was estimated by counting inflorescences, flowers, and, where possible, fruits.

Twenty sample points were established in each plot, located in a stratified-random manner. Each season, the nearest individual of each species under study to each sampling point was flagged and measured over the course of its growth and flowering. To insure an adequate sample of flowering individuals, the nearest flowering individual was also flagged and measured at points where the nearest individual did not flower.

Results were analyzed with the ONEWAY subprogram of the SPSS computer package at the University of Wisconsin-Madison. Differences between 2 treatments were considered significant if the means of the parameter in question fell outside of each other's 95% confidence intervals.

RESULTS

Results from the 1980 and 1981 growing seasons for 3 of the several measured traits are given in Tables 1 to 3. These 3 include estimates of both vigor (numbers of leaves, Table 1) and reproductive response (numbers of flowers, Table 2, and numbers of fruit, Table 3). The data collected in the first 2 years of this study were variable. The authors feel that this variability contributed to the relative lack of statistically insignificant comparisons. Of the 60 cases which were significantly different from the controls, several appear to follow recognizable trends.

Viola pedatifida (prairie violet) exhibited significant increases in the number of leaves per individual (Table 1) and the number of fruit per flowering individual in the early spring and fall burn plots (Table 3). In the late spring burn plot, flowering of *Viola* was eliminated in 1980 and

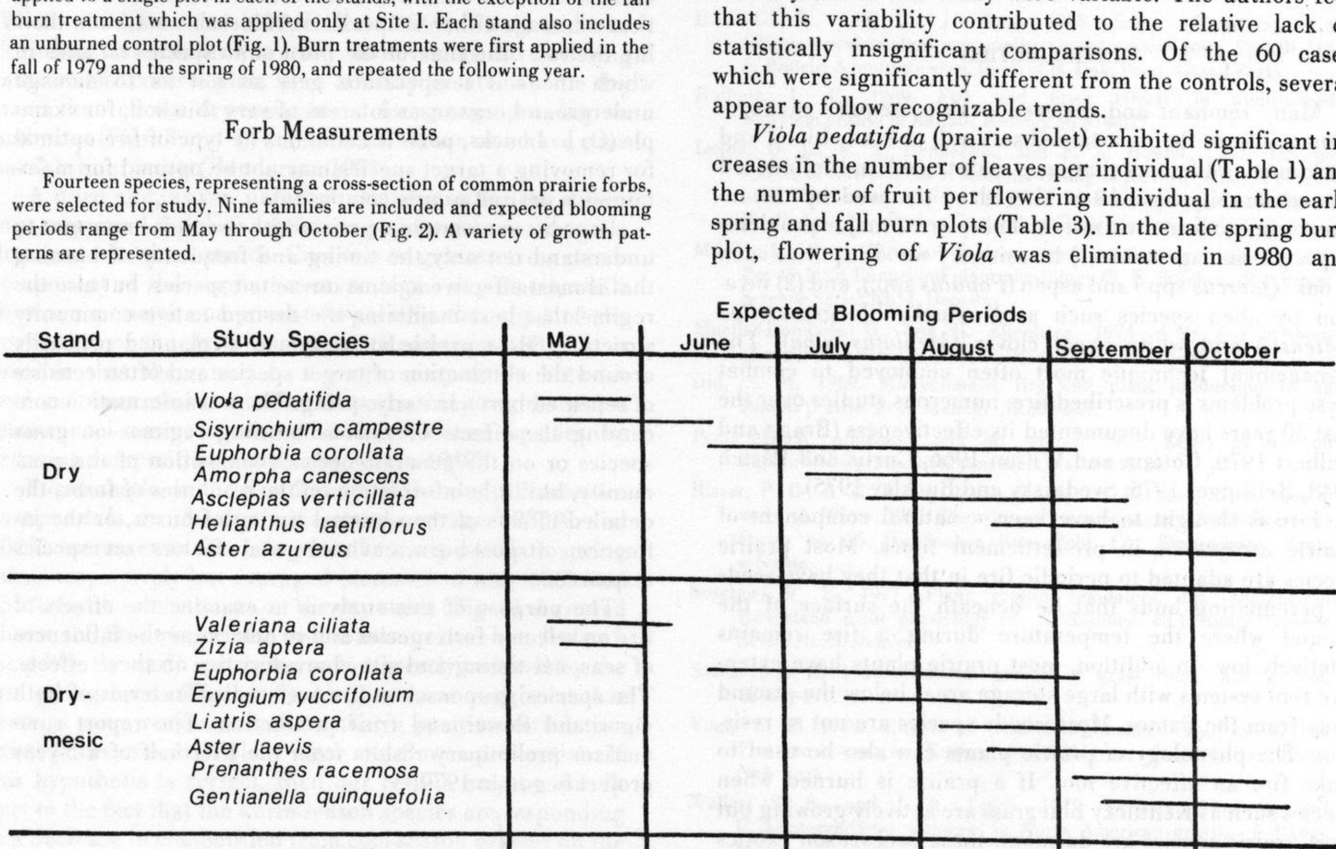

FIG. 2. Expected blooming periods of target species (after Henderson 1981).

TABLE 1. Number of leaves per individual.

		1980				1981			
SPECIES	PRAIRIE STAND	CONTROL	FALL BURN	EARLY SPRING BURN	LATE SPRING BURN	CONTROL	FALL BURN	EARLY SPRING BURN	LATE SPRING BURN
Early-blooming species									
Viola pedatifida	dry	3.05	4.32 + *	3.80*	2.35*	3.60	5.20 + *	4.55 + *	3.45
Sisyrinchium campestre	dry	2.95	4.10	3.00	2.95	0.65	1.30 + *	0.85 +	3.94*
Valeriana ciliata	dry-mesic	2.95		3.00	3.25	3.26		3.90	3.63
	mesic	5.50		6.25	5.05	7.55		7.90	6.55
Zizia aptera	dry-mesic	3.75		3.65	3.42	4.89		3.65	2.78*
	mesic	3.50		4.85*	2.95	2.75		4.90 + *	2.15*
Midsummer-blooming species									
Eryngium yuccifolium	dry-mesic	1.8		1.8	1.9	1.8		1.8 +	2.8
	mesic	4.0		3.4	3.5	4.4		5.0	4.0
Liatris aspera	dry-mesic	1.28		1.88*	2.23*	1.70		2.15 +	2.65*
Late-blooming species									
Aster laevis	dry-mesic					0.55		0.60 +	5.75*
Aster azureus	dry	2.34	2.65	2.31	3.06	4.80	3.25	2.94	5.57
Prenanthes racemosa	dry-mesic	2.1		2.1	2.6				
	mesic	2.6		2.8	3.1				

* discernible from control at .05 level
\+ discernible from late spring burn at .05 level

TABLE 2. Number of flowers per flowering individual.

		1980				1981			
SPECIES	PRAIRIE STAND	CONTROL	FALL BURN	EARLY SPRING BURN	LATE SPRING BURN	CONTROL	FALL BURN	EARLY SPRING BURN	LATE SPRING BURN
Early-blooming species									
Viola pedatifida	dry	1.29	1.70	2.38	n	1.92	1.78 +	1.74	0.33*
Sisyrinchium campestre	dry	2.76	4.83*	4.36*	n	6.00	20.50*	14.20*	n
Valeriana ciliata	dry-mesic	7.55		5.38*	n	6.12		5.10	n
	mesic	9.31		5.69*	n	7.25		6.32	7.20
Zizia aptera	dry-mesic	12.6		13.2	n	35.3		39.4	n
	mesic	12.8		12.5	n	44.6		46.5	n
Midsummer-blooming species									
Euphorbia corollata	dry	91	104	106	91	209	218	246	274
	dry-mesic	9		25	51	48		55	61
	mesic	41		65	55	133		99	132
Amorpha canescens	dry	3.4	7.1 + *	5.8 + *	4.0	4.7	3.4	6.1	5.6
	mesic	4.9		8.5*	8.6*	13.2		9.7	4.5
Eryngium yuccifolium	dry-mesic	n		11.2	14.6	9.8		5.6*	6.2
	mesic	n		17.1	24.0	19.6		12.2*	11.0 *
Helianthus laetiflorus	dry	1.0	1.0	1.0	1.0	1.2	1.2	1.2	1.1
	mesic	1.0		1.4	1.5	1.2		1.0	1.1
Liatris aspera	dry-mesic	14.6		15.9	27.3*	5.9		11.6*	18.3 *
Asclepias verticillata	dry	n	n	n	n	n	n	n	3.3 *
Late-blooming species									
Aster laevis	dry-mesic	16.7		40.8	14.8	15.6		13.7	20.2
Aster azureus	dry	37.9	30.0	27.4 +	14.8*	42.2	52.6	49.3	45.9
Prenanthes racemosa	dry-mesic	61.1		97.5	88.1	42.4		58.0	50.6
	mesic	116.3		110.0	142.0	88.1		70.4	70.6
Gentiana puberula	mesic	5.1		4.5	4.7	3.6		3.3	2.4

* discernible from control at .05 level
\+ discernible from late spring burn at .05 level
n no flowering individuals were found

TABLE 3. Number of fruit per flowering individual

		1980				1981			
SPECIES	PRAIRIE STAND	CONTROL	FALL BURN	EARLY SPRING BURN	LATE SPRING BURN	CONTROL	FALL BURN	EARLY SPRING BURN	LATE SPRING BURN
Early-blooming species									
Viola pedatifida	dry	0.16	0.79 + *	0.75 + *	n	0.33	1.04*	1.21*	0.33
Sisyrinchium campestre	dry	3.8	12.0 + *	7.3 + *	n	3.0	12.8 + *	9.0 + *	n
Zizia aptera	dry-mesic	177		260	n	216		254	n
	mesic	174		277	n	339		227	n
Midsummer-blooming species									
Euphorbia corollata	dry	3.5	1.7	3.4	6.6	41.0	41.2	51.2	40.8
	dry-mesic	0.6		1.0 +	10.8*	9.0		11.4	23.6
	mesic	5.3		13.3	3.7	51.0		56.0	54.0
Asclepias verticillata	dry	n	n	n	n	n	n	n	1.08*
Late-blooming species									
Gentiana puberula	mesic	1.4		1.6	1.6	1.5		1.7	1.6

* discernible from control at .05 level
\+ discernible from late spring burn at .05 level
n no flowering individuals were found

significantly reduced in 1981 (Table 2). Flower and fruit production by *Sisyrinchium campestre* (blue-eyed grass) showed similar responses, increasing significantly in the early spring and fall burn plots and being eliminated in the late spring burn plot (Tables 2, 3). In almost all cases, the flowering of *Valeriana ciliata* (common valerian) and *Zizia aptera* (heart-leaved meadow parsnip) was eliminated in the late spring burn plot (Table 2). *Liatris aspera* (rough blazing star) and *Aster laevis* (smooth blue aster) had significantly more leaves in the late spring burn plot than in the control (Table 1) and *Gentiana puberula* (downy gentian) had significantly shorter flower stems in the late spring burn plot than in the control.

DISCUSSION

The late spring burns, which reduced or eliminated flower and/or fruit production by *Viola pedatifida*, *Sisyrinchium campestre*, *Valeriana ciliata* and *Zizia aptera*, occurred when these species were growing vigorously and had begun to flower. Many spring-blooming species form their flower buds in the fall and will not form new buds to replace those destroyed in a spring fire until the next fall (Butler 1954). Thus the loss of buds may be the most important factor causing the reduction of flowering of these species.

The reduction of the height of *Gentiana puberula* flower stems in the late spring burn plot may also be due to direct damage by the fire. Although this species does not bloom until September (Fig. 2), it begins growth fairly early in the spring, so its young shoots are susceptible to a late spring fire. The plants readily resprout, but the loss of time and energy spent on growth before the fire may mean that they cannot reach the height that they would have achieved had they not been burned.

Environmental conditions immediately following fire may be very favorable for growth, with warmer soil temperature (Black 1968) and possibly even increased nutrient availability (Curtis and Partch 1950, Ehrenreich and Aikman 1963). The observed increases in fruit production by *Viola pedatifida* and in flower and fruit production by *Sisyrinchium campestre* in the late spring burn plot may be a result of ameliorated growing conditions allowing the plants to open more of their already formed flower buds and produce a larger number of fruit. Similarly, the observed increases in number of leaves of *Viola pedatifida* following the fall and early spring burns and of *Liatris aspera* and *Aster laevis* following the late spring burn could be a response to ameliorated growing conditions. We also measured the length of leaves of these species but did not find significant results. It is not clear, then, that the increase in number of leaves produced represents an increase in total leaf tissue or photosynthetic surface. Studies attempting to relate the morphological measures of these species to biomass, currently being conducted, may aid the interpretation of these results.

An alternative explanation for the increase in leaf length of some species is that the fire stimulates bud expansion. Curtis and Partch (1950) have suggested that the heat of the fire on the crown may stimulate growth of *Andropogon gerardii*. Bud expansion could also be stimulated by a hormonal response to loss of growing shoots due to burning.

It appears that the timing of prairie fire may influence the vigor and reproductive response of forb species. Early-blooming species appear to be damaged by late spring fires, and to experience enhanced flowering and fruit production following fall and early spring fires. This pattern is fairly strongly supported by statistically significant results.

Midsummer-blooming species appear to exhibit positive or neutral responses to all burn treatments possibly, in some cases, responding to ameliorated growing conditions. Since these species begin growing late in the spring, they probably suffer little direct damage from even the late spring fires.

The late-blooming species are the most variable in their responses to fire. In some cases, they are similar to the early-blooming species. Since many late-blooming species

have periods of active growth in the spring as well as the fall, these species may be damaged by late spring fires but favored by fall and early spring fires.

Continuing study will examine these postulated relationships further.

ACKNOWLEDGMENTS

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THE ECOLOGY OF SITANION *(GRAMINEAE) IN BENTON COUNTY, WASHINGTON*

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Abstract. Sitanion is widespread in the grasslands of western North America, is taxonomically complex, and exhibits characteristics which make it potentially valuable in land-reclamation efforts in semi-arid regions. The ecology of the genus in the semi-arid region of Benton County was investigated along 1.6-km (1 mile) transects which were selected by a stratified-random procedure. Two species, 1 with 2 varieties, occur in the county. *S. jubatum* occurred at a single site along a grazed roadside at 213 m elevation. *S. hystrix* var. *hordeoides* was found at 2 sites of relatively high elevation (976 and 1098 m) on very coarse substrates, in mechanically disturbed habitats. *S. hystrix* var. *hystrix* occurred at 31 sites, including the 1098-m site of var. *hordeoides* atop Rattlesnake Mountain and a 152-m elevation site close to the Columbia River. All sites of var. *hystrix* were disturbed: along roadsides or by grazing, mowing, cultivation or excavation. Where *S. hystrix* var. *hystrix* occurred, its density varied from 0.1 to 0.76/m^2 and was negatively correlated with both plant height and basal area. Clump basal areas had a mean size of 59.0 cm^2. Culm heights varied between 13-48 cm. The most common associates were *Agropyron spicatum, Artemisia tridentata, Bromus tectorum, Poa sandbergii* and *Sisymbrium altissimum.* This region was not included by Clary (1975) in his ecotypic study of *S. hystrix* and its entire elevational range lies below his lowest collection point (1380 m). The performance of *Sitanion hystrix* var. *hystrix* in Benton County is compared with its performance elsewhere.

INTRODUCTION

***Sitanion hystrix* var. *hystrix* (bottlebrush squirreltail) is a relatively short-lived, perennial bunchgrass of the tribe Triticeae. The genus can be found from the Pacific coast**

eastward into Missouri and from British Columbia southward into Mexico, while in elevation it extends from low-elevation valleys and plains to sub-alpine meadows. It is a component of many communities but is commonly regarded as seral and is associated with disturbance.

The species are highly variable. Controversy over the status of the genus and its infrageneric taxa began with the erection of the genus (Smith 1899). *Sitanion* is closely related to *Agropyron, Elymus,* and *Hordeum* with which it forms intergeneric hybrids (Bowden 1976, Dewey 1967, and Stebbins et al. 1946). Hybridization among species of these 4 genera is sufficiently documented that Wilson (1965) wrote that, while he was "in sympathy with the thesis that *Sitanion* should not be treated as a genus separate from *Elymus*, practicality dictates retention of the name at the present." Hitchcock et al. (1969) gave a similar disclaimer with respect to all 4 of the genera.

Wilson (1963) accepted 4 species in *Sitanion: S. hystrix* with 2 varieties (var. *hystrix* and var. *californicum*); *S. hordeoides, S. jubatum;* and *S. longifolium*. Hitchcock et al. (1969) recognized only 2 species: *S. jubatum* and *S. hystrix*. They relegated Wilson's *S. hordeoides* to varietal status within *S. hystrix*, included *S. longifolium* in *S. hystrix* as var. *brevifolium*, and placed *S. hystrix* var. *californicum* within *S. hystrix* var. *hystrix*. Clary accepted Hitchcock (1950) as the taxonomic authority for his ecotypic analysis of *S. hystrix*. That treatment of the genus recognizes *S. jubatum; S. hystrix*, without varieties; and *S. hansenii*. *Sitanion hansenii* is now regarded as a hybrid between *Elymus glaucus* and either *S. hystrix* or *S. jubatum* (Bowden 1967). We accepted Hitchcock et al. (1969) as the taxonomic authority but the number of interpretations of this taxon necessitates a summary of relevant taxonomies.

Plants were accepted for inclusion in this study if they normally had 2 or 3 spikelets per node and if articulation was below the glumes. These are the criteria employed by Hitchcock et al. (1969) to separate *Sitanion* from *Elymus, Hordeum,* and *Agropyron*. Segregation to sub-generic levels was according to the following, adapted from Hitchcock et al. (1969):

1. Glumes 3 to many-cleft. *S. jubatum*
1. Glumes entire to 2- (rarely 3-) cleft. *S. hystrix*
  2. Spikelets mostly 3 per node, glumes apparently 5 or more per node var. *hordeoides*
  2. Spikelets mostly 2 per node.
    3. Glume-like lemmas absent, glumes simple. var. *brevifolium*
    3. Glume-like lemmas present, at least 1 per node, glumes simple to 2-cleft. var. *hystrix*

A majority of the plants collected (61 of 66) were identified quite readily as *S. hystrix* var. *hystrix*. Two plants, from a single site, were *S. jubatum* and 3 belonged to *S. hystrix* var. *hordeoides*. Two of the 3 came from 1 site which had only var. *hordeoides*; the third came from a site where vars. *hystrix* and *hordeoides* grew together. Because most of the specimens were *S. hystrix* var. *hystrix*, that taxon is the focus of this paper and will be the taxon referred to unless another is explicitly named.

This study developed from the recognized potential of *Sitanion* species for use in revegetating disturbed lands in semi-arid regions, e.g., after mining or in reclaiming eroded lands or severely grazed pastures. While variability in the genus and its abilities for hybridization are established, the frequency of interspecific and intergeneric mix within most local populations is unknown. It seemed worthwhile to study a local population in detail in order to document its taxonomic and ecologic variability. Benton County was taken as the study area because of its proximity to experimental studies conducted by the junior author at the Department of Energy's Hanford Site in south-central Washington and because it offered an adequate population dispersed over a suitably varied landscape. An analysis of the ecologic results are reported here.

Benton County (Fig. 1) is approximately 4405 km² in area and ranges in elevation from 152 m to 1098 m. The area lies well to the northwest of the collection area used by Clary (1975) for his study of ecotypes within *Sitanion*, and the highest elevation in Benton County is lower than the lowest elevation of his collection source (1380 m).

The topography of the county is dominated by basalt layers which form the topographic highs, e.g., Horse Heaven and Rattlesnake Hills (Fig. 1). Lower lands are part of the river basins of the Columbia and Yakima Rivers. Much of the basalt is mantled with a deep loess layer and a variety of erosional and depositional morphologies are superposed on the basalt and loess. Two important examples are scablands close to the Columbia River in the northern third of the county and sand dunes which are scattered throughout the county, but which are frequent at the margins of irrigated lands.

The area lies within the rainshadow of the Cascade Mountains; annual precipitation averages 15.9 cm at the Hanford Meteorology Station. Approximately 43% of the annual precipitation occurs November-January and only 10% is received July-September. In January, the coldest month, the average minimum and maximum temperatures are −3 and 5°C. For July, the warmest month, those values respectively are 16 and 33°C (Thorp and Hinds 1977).

Benton County lies wholly within the *Artemisia tridentata-Agropyron* Zone of the Steppe Region of Washington as described by Daubenmire (1970). Küchler (1964) classified the areas as Sagebrush Steppe, but the region is locally referred to as desert. Dryland wheat farming and cattle grazing are the dominant land uses, but significant acreages are retained both in relatively intact steppe and in irrigated agriculture. Most of the better steppe vegetation is within the Hanford Reservation, and especially within the Arid Lands Ecology (ALE) Reserve. Irrigated agriculture commands most of the land within the

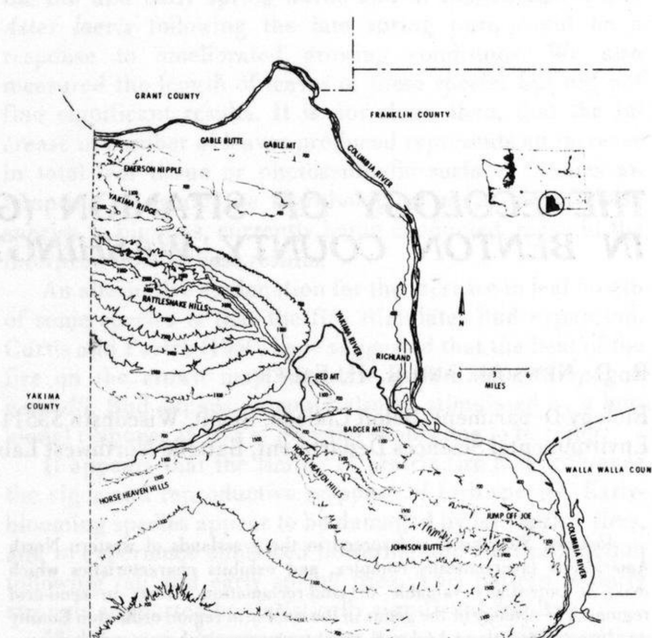

FIG. 1. The main topographic features of Benton County and its location in Washington.

Yakima River valley where alfalfa, grapes, hops, mint, and orchards are important crops. Agriculture is increasing in the Horse Heaven Hills, where wheat is the main crop. Urban land is a minor category. The transects used in this study passed through all land-use categories.

METHODS

Methods used in this study provided a taxonomic and an ecologic assessment of the total *Sitanion* population within Benton County. Morphologic and habitat variations, and correlated patterns between these variables, were ascertained. Sites and plants were selected for study according to stratified-random procedures.

Square-mile sections of the county were numbered and 45 numbers were drawn at random, with no opportunity for a number to be drawn twice. Additionally, the more significant topographic features of the county were divided on an altitudinal basis and 10 more random points were selected within 400 ft-elevational (130 m) intervals.

For the randomly chosen points, the northwest corner of a selected section marked the beginning of a 1.6-km (1 mi) transect. A transect was used in order to include heterogeneity (ecologic and taxonomic) in each sample. Transects were laid out along straight paths which offered the more promising opportunities for finding *Sitanion*. Ordinarily, this meant selection of a line of travel close to the diagonal of the section but it always meant selection for a diversity of habitats. Since the goal was to locate as many populations of *Sitanion* as possible, within the bounds of the random procedures, it was judged inappropriate to adhere rigidly to predetermined compass directions because that criterion often would lay the transects across unprofitable areas, e.g., wholly within cultivated lands, over precipitous cliffs, out of the county, or onto paved, industrial, or otherwise continuously-disturbed lands.

For the stratified-random points, the starting point was at the prescribed altitude at whatever access point it could be reached. The 1.6-km transect was divided such that the starting point became the mid-point of the transect, with half laid to either side of the point and along the prescribed contour.

The transects were walked, looking for *Sitanion* within about 3 m on either side of the line of traverse, until either *Sitanion* was found or the end of the transect was reached. A compass, altimeter, and topographic map provided information about the *Sitanion* habitats. *Sitanion* is a reasonably distinctive plant, especially when it bears inflorescences and these were present throughout the field season. However, clumps of *Agropyron, Elymus* and *Hordeum* were usually checked to be certain that *Sitanion* was not being passed by. It is assumed that any plants of *Sitanion* that occurred along a transect were discovered.

The first *Sitanion* found along a transect was taken as a sample plant. If others were within 10 m of the sample plant, they were regarded as part of a "very local" population and 1 or more of them (to 6, depending on population size and variability) were taken as additional sample plants. These 10-m-radius areas are the "sites" referred to hereafter. The number of *Sitanion* plants within a site determined the species density. Altitude, topographic position, general nature of the habitat, and evidence of disturbance were recorded for each site. All vascular species within a site were recorded for presence. A pooled soil sample, consisting of 3 6-inch-deep subsamples, was taken at each site and analyzed for the variables listed in Tables 2 and 3. Soil analyses were conducted by U.S. Testing, Richland, Washington.

Sample plants were scored in the field for 5 additional attributes: culm and leaf heights, numbers of flowering and non-flowering culms, and clump basal area. Other variables were scored later. Sample plants were collected and later deposited as voucher specimens in the Ownbey Herbarium at Washington State University, Pullman.

After completing the sampling of 1 very local population, the walk of the transect was continued and subsequent very local populations were handled in like manner until the end of the transect was reached. Field work was conducted June-August 1976. Nomenclature is according to Hitchcock et al. 1969.

RESULTS

Sitanion was found on 23 of the 54 transects (42.6%). Thirteen transects had 1 very local population and 10 had 2, yielding 33 sites. *Sitanion* almost always was associated with physical disturbance of the substrate. Of the 33 sites, 16 (48.5%) were in grazed or otherwise disturbed grasslands; 8 (24.2%) were at the edge of a road or farm lane; 7 (21.2%) were on rocky hill crests; and 2 (6.0%) were on plowed land.

Sitanion hystrix var. *hystrix* was the only *Sitanion* taxon at 30 of the sites. *S. hystrix* var. *hordeoides* and *S. jubatum* occurred as the sole *Sitanion* taxon at one site each, and one site supported a mixed population of varieties *hystrix* and *hordeoides.*

Thirty-six vascular species were found in close proximity to *Sitanion,* but most species occurred at only 1 or 2 of the 33 sites. Those which occurred in at least 5 sites are listed in Table 1.

Summary statistics for all measured biotic and habitat variables are presented in Table 2. *Sitanion* density is reported in numbers per m², which expresses density within the *Sitanion* sites. Extrapolation from this unit to numbers per ha is not warranted because on several sites only a single *Sitanion* plant occurred, and in other cases extensive searching out from the 1 or 2 populations found along the transect failed to reveal any other populations.

Eight habitat variables were significantly and positively intercorrelated: CEC, % Clay, Magnesium, % Silt, % Organic Matter, Total Bases, Calcium, and Elevation (Table 3). Additionally, both CEC and Clay were negatively correlated with Sand; Silt and Organic matter were positively correlated with Potassium; Organic Matter was negatively correlated with pH; and Total Bases and Calcium were positively correlated with both Base Saturation and *p*H.

In addition, Potassium was positively correlated with Silt and Organic Matter and negatively correlated with Sodium and Sand. Base Saturation was positively correlated with *p*H. Sodium was negatively correlated with Potassium and had no significant correlations with anything else measured. Sand had no positive correlations among the variables studied, but was negatively correlated with all factors except sodium and *p*H.

The results of stepwise multiple regression (MR) are presented in Table 4, together with the significant correlations among measured biotic variables. Culm and Leaf Heights, Basal Area, and Number of Flowering Culms all were significantly and positively intercorrelated, and all were negatively correlated with *Sitanion* density but their responses to habitat variables differed.

Each of the 10 steps of multiple regression was significant in the analysis of Culm and Leaf Heights and the ac-

TABLE 1. Percent presence values of angiosperm species which occurred at 5 or more *Sitanion* sites.

SPECIES	COMMON NAME	% PRESENCE
Agropyron spicatum	bluebunch wheatgrass	18.8
Artemisia tridentata	big sagebrush	42.0
Balsamorrhiza careyana	balsam-root	10.1
Bromus tectorum	cheatgrass	89.9
Poa sandbergii	Sandberg's bluegrass	40.6
Salsola kali	Russian thistle	18.8
Sisymbrium altissimum	tumble mustard	24.6
Triticum aestivum	wheat	7.2

TABLE 2. Summary statistics for plant and habitat variables. Soil properties expressed in % oven-dry weight (except Base Saturation). CEC = Cation Exchange Capacity.

Plant Variables	Range	Mean	S.D.
Culm height (cm)	13.0 - 48.0	26.5	7.8
Leaf height (cm)	11.0 - 51.0	30.8	8.2
Basal area (cm^2)	1.0 - 296.0	59.0	18.2
Number of flowering culms	4 - 119	40.5	27.8
Number of internodes below inflorescence	2 - 5	3.7	0.6
Density (No./m^2)	0.1 - 0.76	0.27	0.23
Habitat Variables			
Clay (%)	6.0 - 22.8	11.2	4.0
Silt (%)	18.3 - 56.4	34.7	10.3
Sand (%)	29.1 - 76.2	54.4	12.7
Organic matter (%)	0.5 - 2.9	1.2	0.5
CEC (meq/100 gm)	5.0 - 26.0	11.6	5.3
Mg^{++} (meq/100 gm)	0.6 - 5.5	1.8	1.1
Ca^{++} (meq/100 gm)	3.2 - 27.2	10.1	6.9
K^+ (meq/100 gm)	0.6 - 2.7	1.3	0.5
Na^+ (meq/100 gm)	0.1 - 0.5	0.2	0.1
Total bases (meq/100 gm)	5.0 - 31.2	13.2	7.6
Base saturation (%)	61.2 - 137.4	109.5	33.5
pH	6.5 - 8.3	7.8	4.1
Elevation (meters)	152 -1098	302	249

cumulated R^2 values were 56% and 55%, respectively. The rank of apparent importance of the habitat variables differed, however, with Clay being the most important in explaining the variance in Culm Height ($R^2 = 31\%$) and Magnesium being most important for Leaf Height ($R^2 = 28\%$). Base Saturation, which is not part of the tightly correlated habitat variables, was second in importance in MR analysis in explaining variance in Culm Height and third in importance for Leaf Height. Both height measurements were negatively correlated with several habitat factors, including Clay, Magnesium, CEC, Calcium, and Base Saturation and were positively correlated only with Sand.

The Basal Area of *Sitanion* plants was not significantly correlated with any of the measured habitat variables and none of the steps of its MR were significant. The accumulated R^2 in this case was 22%.

The Number of Flowering Culms, while significantly correlated with Culm and Leaf Heights, as well as with Basal Area, showed stronger correlation with Basal Area than with the other variables. Its only significant correlation with habitat variables was with Elevation. Four steps of the MR were significant, but together these explained only 19% of the variance in the Number of Flowering Culms. The accumulated R^2 for all 10 steps was 27%.

The Number of Internodes below the Inflorescence was negatively correlated with the Number of Flowering Culms, and with both CEC and Elevation. It was not correlated with either measurement of plant height. The first step of MR was the only significant step and yielded an $R^2 = 10\%$. The accumulation R^2 for all 10 steps was 29%.

Sitanion density showed no positive correlation with any measured plant factor, but was negatively correlated with 4 of the measured plant variables. In contrast, it was positively correlated with 7 of the measured habitat variables (Table 4), and 10 steps of the MR against density were significant. Clay, Organic Matter, and Base Saturation were the 3 most important variables identified by MR, with R^2 values of 35%, 47%, and 50% respectively. The 10 steps yielded an accumulated R^2 of 63%.

DISCUSSION

Sitanion hystrix has pioneer capabilities and its presence usually signifies physical disturbance, although the magnitude of the disturbance can be small, e.g. that of an animal burrow. This species, and the genus in general, is potentially weedy. How great the potential is, is not clear because its performance on general landscapes is largely unstudied. Interest in the taxon for land reclamation purposes relies, in part, on its pioneer qualities but such interest also depends on its genetic and hybridizing characteristics.

The limits of tolerance of *S. hystrix* to disturbance are not known. Absence, of course, is not evidence of intolerance for conditions of a site. However, 2 kinds of disturbed situations from which *Sitanion* was always absent in this study are worth reporting. The genus was never found on even moderately wet sites, e.g., on lowlands along the rivers or on damp soil along irrigation canals. It also did not occur on any of the areas of unstabilized sand that were examined but did occur on bare gravel.

The presence of *Sitanion* on only 23 of the 54 transects examined in this study, and at only 33 sites on those transects, is indicative of its rarity on this landscape. Rickard, Cline, and Gilbert (1973) listed *Sitanion hystrix* as being "scattered" in their study fields within the county. Daubenmire's (1970) characterization of habitat types within the steppe region of Washington includes the comment, pertinent to Benton County and to a large region of

TABLE 3. Product-moment correlation coefficients between measured habitat variables. CEC = Cation Exchange Capacity. O.M. = % soil organic matter. T-Base. = total bases in soil. B-Sat. = % base saturation of soil. Values greater than 0.27 and 0.35 are significant at probability levels, respectively, of 0.05 and 0.01.

	CEC	Mg^{++}	Clay	Silt	O.M.	Elev.	T-Base.	Ca^{++}	K^+	B-sat.	pH	Na^+	Sand
CEC	---	.88	.91	.79	.60	.80	.78	.70	.09	.16	.08	.06	-.84
Mg^{++}		----	.84	.74	.54	.82	.55	.44	-.02	-.05	-.12	.11	-.77
Clay			----	.73	.50	.75	.71	.63	.19	.16	.03	-.03	-.83
Silt				----	.60	.64	.64	.56	.30	.11	.07	.05	-.98
OM					----	.50	.40	.32	.39	.03	-.28	-.12	-.62
Elevation						----	.39	.31	-.16	-.17	-.22	.23	-.66
Total Bases							----	.99	.23	.69	.46	-.11	-.71
Ca^{++}								----	.17	.74	.52	-.11	-.63
K^+									----	.21	.06	-.35	-.34
Base Satur.										----	.55	-.20	-.16
pH											----	-.17	-.09
Na^+												----	.00
Sand													----

TABLE 4. Significant intercorrelations with biotic factors. Column a lists product-moment correlation values which are significant. Values greater than 0.27 and 0.35 are significant at probability levels of 0.05 and 0.01 respectively. Column b gives the rank of habitat variables for significant steps in multiple regression of habitat × plant variables, * = significant at 0.05 level; ** = significant at 0.01 level.

	Culm Height		Leaf Height		Basal Area		No. Culms		No. I-nodes		Density	
	a	b	a	b	a	b	a	b	a	b	a	b
Culm Height	--		.92		.47		.47		--		-.62	
Leaf Length	.92		--		.56		.44		--		-.60	
Basal Area	.47		.56		--		.66				-.37	
No. Flr. Culms	.47		.44		.66		--		-.35			
No. I-nodes	--		--				-.35		--			
Density	-.62		-.60		-.37		--		--		--	
CEC	-.53	7**	-.50	7**	--		--		-.30		.49	5**
Mg^{++}	-.52	3**	-.53	1**	--		--	4*	--		.44	9**
Clay	-.55	1**	-.53	5**	--		--	2*	--		.59	1**
Silt	-.32	6**	--	4**	--		--		--		.37	7**
O.M.	--	4**	--	2**	--		--	3*	--		--	2**
Elevation	-.30	5**	-.36	8**	--		.31	1*	-.31	1*	.38	
Total Bases	-.48	8*	-.39		--		--		--		.45	
Ca^{++}	-.44		-.35	9*	--		--		--		.42	4**
K^{+}	--		--	10**	--		--		--		--	6**
Base Satur.	--	2**	--	3**	--		--		--		--	3**
pH	--	9**	--	6**	--		--		--		--	10**
Na^{+}	--		--		--		--		--		--	
Sand	.39	10**	.30		--		--		--		-.43	8**

central Washington, that *Sitanion* is "seldom abundant except along roadsides and where topsoil has been scraped away." Daubenmire gives quantitative measures of plant cover for many species, but for *Sitanion hystrix* cover is given as "trace."

The density of *Sitanion* is seldom reported but figures from 2 studies are available for comparison with those of this study. Harness and West (1973) reported average densities of *Sitanion* between 1.25 and 1.89/m² on formerly grazed sites in southeastern Idaho. Tueller (personal communication 1982) found a range of 0.2-9.8/m², with a mean density of 4.6/m² for *Sitanion hystrix* in the Owyhee desert in north central Nevada. By comparison, the range and mean density of *Sitanion hystrix* found in this study were low (Table 2).

When *Sitanion* density is not given, its importance in the community often is qualitatively implied. Eddleman (1979), for example, lists *Sitanion hystrix* as "important" in southeastern Montana communities, and Reid (1941) ranks the genus among the "most important secondary species" of subalpine grasslands of the Blue and Wallowa Mountains of eastern Oregon. At apparently higher levels of prominence, Hironaka and Tisdale (1963) mark *Sitanion hystrix* among the "most abundant perennial grasses," and Wright and Klemmedson (1965) cite the species as a subdominant in certain communities, both in southern Idaho studies. Franklin and Dyrness (1973) report the species as one of the "principal" grasses of openings in the lodgepole pine zone, and as the "third-ranked dominant" of certain grassy meadows, in eastern Oregon. Finally, Tueller and Blackburn (1974) describe *S. hystrix* as a "dominant" on sites of poor conditions in Nevada.

Sitanion, thus, appears to be lower in prominence in Benton County, and perhaps in most of central Washington, than it is elsewhere. Is this because it occupies fewer of the sites available to it, and, if so, is that because of biotic interaction or because of abiotic factors? Another possibility is that ecotypic differences are involved. Individuals within the county are robust and fertile, and seem not to be close to any limit of tolerance.

Where *Sitanion hystrix* was present in Benton County, plant density was negatively correlated with individual plant size, and these characters responded differently to habitat factors (Table 4). Density was positively correlated with several interrelated soil factors, among which clay, silt, and both cation quantity and variety seem particularly important. The significant negative correlation between density and sand, then, was expected but the positive correlation between plant height and sand was not.

Plant basal area, another good measure of plant size, was also negatively correlated with *Sitanion* density but showed no correlations with measured habitat variables. Basal area could be linked to plant age, which is unknown, or it could be a function of an unmeasured variable, of which there are many. It is interesting that *Sitanion* density and height, respectively, were positively and negatively correlated with an increase in elevation, while basal area showed no correlation. Precipitation increases with altitude (Thorp and Hinds 1977) in the Rattlesnake Hills (Fig. 1) and it could be that higher rainfall promotes an increase in density which, in turn, dampens growth in height. Other habitat variables which correlated positively with density also correlated positively with an increase in elevation and, hence, are not complicating factors in this hypothesis. The hypothesis that increased density of *Sitanion hystrix* slows growth, and that habitat conditions affect growth indirectly, is speculative, especially considering the low densities discovered in this study, but fits the available data. It would be instructive to know the relationship between plant density and size under conditions of greater density.

Variation in the Number of Internodes below the inflorescence was not explained by data gathered in this study, but it is interesting that it shows no correlation with culm height. Possibly its negative correlations with CEC, elevation, and number of flowering culms are spurious and the factor may be principally under genetic control or the result of unmeasured variables.

One attribute which recommends *Sitanion* for land reclamation is its high vigor during drought (Eddleman 1979). Further, its seeds require no afterripening (Young and Evans 1977) and, hence, will germinate soon after collecting and dispersing. It tolerates a broad spectrum of rock and other substrate types, showing a slight affinity for noncarbonate rocks (Marchand 1973) and preference for soils of high clay content rather than of sand (Wright 1967, Wright and Klemmedson 1965). Our own results are mixed with respect to this latter point. We noted its absence on dune sands but found a positive correlation between plant height and increased sand on other sites. Culm heights reached 35 cm, well above the average, on soils of 76% sand, the highest sand content we found. *Sitanion* density in this case was 0.4/m² (above average) and basal area was 12 cm² (below average). The relationship with sand may be a matter of seedling establishment. Poor seedling success would cause a low density but those which did establish might have access to more favorable nutrient or moisture supply than other substrates provide.

Additionally, the species withstands burning (Wright and Klemmedson 1965, Wright 1971) and it has some competitive ability. Hironaka and Tisdale (1963) report an increase in *Sitanion hystrix* over a 20-year period on formerly grazed pastures in southern Idaho which had been invaded by *Bromus tectorum* (cheatgrass) soon after the cessation of grazing. Also, Reid (1941) discovered that *Sitanion hystrix* invaded native subalpine meadows in eastern Oregon under grazing pressure and increased in frequency after grazing ceased. An ability to compete with *Kochia scoparia* (summer cypress) and with *Bromus japonicus* (Japanese brome) in eastern Montana was reported for *S. hystrix* by Eddleman (1979), and Hironaka and Sindelar (1973) found that it established well when seeds were broadcast into stands of *Elymus caput-medusae* (medusahead).

These properties all are desired in a species selected for reclamation work but the degree to which they are vested throughout *Sitanion hystrix* needs further study. Taxonomic variation within the species is considerable and its ecologic variability might be equally great. Wright and Klemmedson (1965) mention the solid culm of *Sitanion hystrix* as being important in resistance to fire. We found a solid culm only in *Sitanion jubatum* after careful examination of all voucher specimens and of many plants not collected. Wright (1970) lists the number of non-flowering culms as the second best predictor of yield (dry weight of the plant). We found no non-flowering culms. From the smallest, greenest plant to the largest, half-dead clump encountered in this study, culms of all sizes produced flowers. In the matter of disarticulation, Hironaka and Tisdale (1963) mention the ability of the species to disperse seed because the entire seed head is blown about intact. Our common observation was that spikelets disarticulated below the glumes, breaking the rachis, and our recognition of the species depended, in part, upon this being true. That does not mean that heads could not be dispersed intact but it raises a question worth clarification.

Sitanion hystrix east of the Rocky Mountains has segregated ecotypically (Clary 1975), and apparently throughout the range of *Sitanion*, intergeneric hybrids are formed among species of a 4-genus complex (Bowden 1967). But the contribution to local populations of such segregation and crossing, and the pattern of change in such contribution throughout the range of the species, are yet to be investigated. The degree to which the results of this study apply only to *Sitanion hystrix* var. *hystrix* as delimited in this study, versus applying to the entire species, cannot be determined from the literature.

In summary, the genetic and taxonomic variability ascribed to *Sitanion hystrix* makes detailed study and point-by-point comparison of ecologic performance necessary. Local populations need characterization, both taxonomically and ecologically. It would be helpful to be able to compare similarly defined taxa from throughout their ranges. *Sitanion hystrix* illustrates, perhaps in an exceptional manner, just how formidable is the task of bringing our understanding of species and of ecosystems to a predictive level.

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THE EFFECTS OF FIRE, LITTER, AND ASH ON FLOWERING IN ANDROPOGON GERARDII

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Abstract. The objective of this study was to evaluate the relative importance of the direct effects of burning on inflorescence production in *Andropogon gerardii.* Major treatments used included all possible combinations of presence and absence of fire, litter, and ash. The environmental variables measured included soil moisture, soil temperature, available soil nitrogen, and amount of light at the soil surface. Soil moisture was significantly less on burned plots than on unburned plots. No significant differences in available soil nitrogen were observed. Soil temperatures were significantly higher and light at the soil surface was increased when the organic material was removed. Inflorescences per m² of canopy cover was significantly increased by the presence of fire. Litter removal and addition of ash did not significantly affect inflorescence production. The results indicate for the first time that the presence of fire itself was a more important environmental cue for increased flowering than removal of litter or addition of ash by burning.

INTRODUCTION

Studies have shown that burning and removal of organic material increase flowering in many warm-season grasses, including *Andropogon gerardii* (big bluestem) (Aikman 1955, Blake 1935, Burton 1944, Cornelius 1950, Curtis and Partch 1950, Dix and Butler 1954, Ehrenreich 1959, Ehrenreich and Aikman 1957, Ehrenreich and Aikman 1963, Hadley and Kieckhefer 1963, Kucera and Ehrenreich 1962, Old 1969, Rice and Parenti 1978). Removal of organic material may affect flowering through increased soil temperature (Curtis and Partch 1950, Ehrenreich 1959, Ehrenreich and Aikman 1963, Kucera and Ehrenreich 1962, Old 1969), increased available light (Kucera and Ehrenreich 1962, Old 1969), decreased soil moisture (Ehrenreich and Aikman 1963), and removal of allelopathic chemicals (Rice and Parenti 1978). Removal of much of the standing dead, litter, and living material is just 1 of the effects of burning. It also provides charred organic material and ash from the organic material burned and produces heat. Most previous studies have attributed the increase in flowering due to burning to the removal of litter; however, they contain no evidence that the ash and heat produced by fire are not important. Addition of charred organic material and ash may darken the soil surface, thus increasing soil temperature (Ehrenreich 1959, Kucera and Ehrenreich 1962) and increase available nutrients (Curtis and Partch 1950, Ehrenreich and Aikman 1963, Kucera and Ehrenreich 1962). The heat of the fire may destroy allelopathic or inhibitory chemicals (Rice and Parenti 1978). The objective of this study was to separate the effects of litter, fire, and ash on flowering in *Andropogon gerardii.*

MATERIALS AND METHODS

This study was carried out April-September 1978 on Konza Prairie Research Natural Area (KPRNA) located 12 km south of Manhattan, Kansas. KPRNA encompasses 3487 ha of native tallgrass prairie in the Kansas Flinthills. The study site was located in a lowland area on Tully soil—a fine, mixed, mesic Pachic Argiustoll. The area was last burned 3 years earlier on 30 April 1975. Standing dead and litter accumulation was substantial.

Experimental Design

This study was a 3-way factorial experiment incorporating all possible combinations of presence and absence of litter, fire, and ash (Table 1). The use of these combinations allows one to separate the effects of litter, ash, and presence of fire, and assess interactions between these. In addition to these treatments some plots were burned in April to determine the effects of season of burning (Table 1). To assess the effects of darker soil surface due to burning, sand was added to 2 × 2 m areas on each April-burned, ash-left plot to match closely the color of the soil surface to that of the litter.

All treatments except those with sand added were applied to 5 × 5 m plots. The plots were arranged in a 4 × 22 plot grid with every other plot unused in an effort to minimize the effects of runoff from 1 treatment into the next. Plots were separated by a 1.5-m mowed strip. Four replications of each treatment were used, with the exception of mowed, mulch removed, ash added and mowed, mulch left, ash added. Three replications of these 2 treatments were used. The treatments were randomized to the plots. May-burned plots were done as split plots with litter added to the north half of the plots. May-burned plots were burned 11 May 1978, ash was removed the same day, and litter was put back 13 May 1978. April-burned plots were burned 27 April 1978. All burned plots were burned with the wind. Plots were mowed 26 April 1978 with a rotary blade mower. The organic material was cut into small pieces 5-10 cm long. This material will be referred to as mulch. The organic material added to the burned plots was cut with a sickle-bar mower. This material was cut at 2-3 cm above ground, but was otherwise left intact. This material will be referred to as litter. The sickle-bar mower was not used for all plots because of equipment failure. Ash was removed by vacuuming with a gasoline-powered vacuum. The ash was collected and applied to the mowed, ash-added plots.

TABLE 1. Mean inflorescence density for different treatments (± standard errors).

TREATMENT	INFLORESCENCES m^{-2} OF CANOPY COVER
Unaltered control	1.1 ± 0.5
Mowed, mulch left	9.6 ± 2.0
Mowed, mulch left, ash added	11.8 ± 1.1
Mowed, mulch removed	13.8 ± 5.4
Mowed, mulch removed, ash added	11.1 ± 3.0
May-burned, ash left	23.2 ± 4.3
May-burned, ash left, litter added	14.0 ± 3.4
May-burned, ash removed	23.4 ± 5.3
May-burned, ash removed, litter added	31.6 ± 4.4
April-burned, ash left	28.0 ± 4.4
April-burned, ash left, litter added	21.3 ± 3.8
April-burned, ash left, sand added	29.1 ± 5.9

TABLE 2. Percent soil moisture at different soil depths on 8 August 1978 (Mean of 3 replicates ± standard errors). Numbers with the same letters are not significantly different at the 0.05 level.

	PERCENT SOIL MOISTURE BY SITE		
SOIL DEPTH (CM)	UNBURNED SITE (MORE THAN 10 M FROM BURNED SITE)	UNBURNED SITE (WITHIN 2 M OF BURNED SITE)	BURNED SITE
0 - 10	27.99 ± 2.00a	21.54 ± 2.82a	14.04 ± 0.42b
20 - 30	20.76 ± 2.48a	20.28 ± 2.99a	12.50 ± 1.45b
40 - 50	20.86 ± 1.74a	18.56 ± 0.65a,b	14.49 ± 1.62b
60 - 70	20.10 ± 1.52b	16.34 ± 0.49a,b	14.56 ± 0.46b
80 - 90	17.70 ± 2.22a	15.04 ± 0.75a	12.59 ± 0.52a
100-110	17.54 ± 1.53a	16.17 ± 0.50a	14.49 ± 0.70a
120 - 130	17.78 ± 0.89a	17.96 ± 1.09a	15.83 ± 0.80a
140 - 150	18.90 ± 0.94a	19.01 ± 0.25a	17.96 ± 0.90a

Variables Measured

Light. On 25 May 1978 a Weston photometer with a quartz filter photoelectric cell was used to determine percent of total available visible light that reached the soil surface and was reflected by it. Light absorbed by the soil surface was determined by subtraction.

Soil moisture. Soil moisture was measured on 9 August 1978 by taking a 1.5-m-deep soil core and gravimetrically determining soil moisture for every other decimeter by drying at 105°C (Table 2). Soil moisture was measured on April-burned plots with ash left, adjacent unaltered plots, and unaltered plots further than 10 m from burned plots (Table 2).

Soil nitrogen. Available nitrate and nitrite nitrogen were determined in core sections not used for soil moisture (Table 3). Soil nitrogen (NO_2^- and NO_3^-) was determined by the method of Lowe and Hamilton (1967).

Soil temperature. Soil temperatures were measured in early afternoon 7 times throughout the growing season. Surface soil temperatures were approximated with a mercury thermometer; 10 cm- and 30 cm-deep temperatures were measured with dial thermometers. One temperature was measured at each depth per plot. Temperatures were measured at random locations along transects on the north sides of the plots.

Sexual reproductive effort. Sexual reproductive effort was measured on 17-18 October 1978 in several ways. Inflorescence density and height were measured along a transect located at random within the plots. Twenty inflorescences were collected along the transect and spike weight and seeds per spike were determined from these. All inflorescences had only 1 spike.

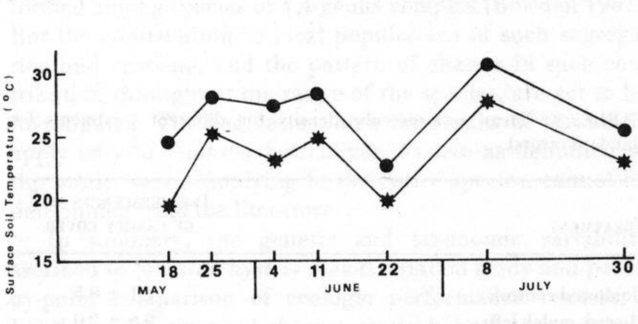

FIG. 1. Effect of litter on surface and 10 cm-deep soil temperatures.

TABLE 3. Available soil nitrogen at different soil depths on 8 August 1978 (Mean of 3 replicates ± standard errors). Numbers with the same letter are not significantly different at the 0.05 level.

	AVAILABLE SOIL NITROGEN BY SITE (nM (NO_2^- + NO_3^-))		
SOIL DEPTH (CM)	UNBURNED SITE (MORE THAN 10 M FROM BURNED SITE)	UNBURNED SITE (WITHIN 2 M OF BURNED SITE)	BURNED SITE
10 - 20	39.63 ± 6.36a	52.08 ± 10.22a	27.66 ± 4.28a
30 - 40	33.98 ± 2.35a	48.67 ± 7.47b	33.01 ± 2.17a
50 - 60	41.92 ± 1.77a	34.20 ± 8.92a	31.70 ± 5.03a
70 - 80	37.37 ± 2.64a	43.26 ± 9.35a	37.56 ± 1.42a

The amount of *Andropogon gerardii* in each plot was highly variable. To reduce the within-treatments variability, the percent canopy cover of *Andropogon gerardii* was estimated and inflorescences per m² (m^{-2}) of canopy cover was calculated (inflorescences m^{-2} of canopy cover = inflorescences m^{-2} × 100/percent canopy cover). Canopy coverage was estimated on 10 m² quadrats in each plot on 14 and 17 September 1979. Only results for inflorescences m^{-2} of canopy cover are given.

RESULTS

Light. The soil surface received less than 10% of visible light on plots with litter or mulch. Before growth started, the soil surface on plots without litter or mulch received 100% of the visible light and reflected less than 10% of it (Table 4).

Soil moisture and nitrogen. Burned areas had significantly less moisture than adjacent unburned areas to a depth of 30 cm ($P < 0.05$) and less than distant unburned areas to a depth of 70 cm ($P < 0.05$) (Table 2). Unburned areas adjacent to burned plots showed consistently lower soil moisture than those areas away from burned plots, but these differences were not statistically significant ($P > 0.05$) (Table 2). No significant differences in nitrogen between treatments were observed ($P > 0.05$) (Table 3).

Soil temperature. The 3-way factorial analysis of variance using May-burned plots indicates that litter removal significantly raised surface soil temperatures and 10 cm-deep temperatures throughout the growing season (Fig. 1). The effect on 30 cm-deep temperatures was less pronounced, but they followed the same trend. Presence of fire and addition of ash or sand did not significantly affect soil temperatures ($P > 0.05$). Interactions between treatments

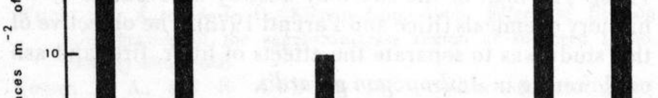

FIG. 2. Effects of fire, litter, and ash on inflorescence density in *Andropogon gerardii.*

TABLE 4. Percent of total sunlight reaching the soil surface and absorbed by it under different treatments. "–" = not evaluated because of absence of litter.

Treatments	Incoming light (foot-candles)	% Light reflected	% Light absorbed by litter	% Light passed through	% Light absorbed by soil
Burned, ash removed	5100	3.92	–	–	96.08
Burned, ash removed, litter added	5200	8.08	91.59	0.33	0.33
Burned, ash left	8000	4.38	–	–	95.62
Burned, ash left, sand added	7200	5.00	–	–	95.00
Mowed, mulch left	3000	6.33	90.34	3.33	3.33
Mowed, mulch removed	9100	7.69	–	–	92.31

were not significant ($P > 0.05$). April-burned plots showed the same trends.

Sexual reproductive effort. The only index of sexual reproductive effort which was significantly affected by the treatments in this study was inflorescences m^{-2} of canopy cover. Inflorescence density was significantly increased by the presence of fire in both April- and May-burned plots ($P=0.002$ and $P=0.0005$, respectively) (Fig. 2). The increase in inflorescence density associated with litter removal was not significant ($P > 0.05$) (Fig. 2). However, mowed plots with the mulch left had significantly greater inflorescence density than unaltered plots ($P=0.007$) (Fig. 3). Presence of ash actually resulted in a decrease in inflorescence density, also not significant ($P > 0.05$) (Fig. 2). Time of burning and addition of sand did not significantly affect inflorescence density ($P > 0.05$) (Fig. 3). Interactions between treatments were not significant ($P > 0.05$). Differences in soil moisture, soil temperature, and light due to the treatments were not significantly correlated with differences in flowering ($P > 0.05$).

DISCUSSION

Most previous authors have concluded that litter removal by burning was the most important factor affecting inflorescence production (Aikman 1955, Curtis and Partch 1950, Ehrenreich 1959, Kucera and Ehrenreich 1962, Old 1969, Rice and Parenti 1978). This conclusion is based on other studies such as Weaver and Rowland (1952), showing that litter removal by mowing and/or raking caused a significant increase in seed production over unmowed areas. This study also indicates that removal of organic material may be an important factor, because cutting the organic material increased inflorescence production when compared to plots where the organic material remained intact. However, in this study the presence of fire was a more important environmental cue for increasing flowering in *Andropogon gerardii.* The results of some previous studies are consistent with this finding. Although Curtis and Partch (1950) found the greatest difference in inflorescence density between plots with and without litter, they did find that burned plots had greater inflorescence density than unburned plots. Although the differences are not significant, Rice and Parenti (1978) noted greater inflorescence production on burned than mowed and unaltered plots. They attributed increased dry matter production on burned and mowed plots to higher soil temperatures early in the season; however, this does not account for the difference in inflorescence density since their soil temperatures were lower on burned than mowed plots. In the present study no relationship could be found between inflorescence production and soil temperature. Therefore burning may increase flowering in a different way than it increases primary production.

While there may be other direct effects of burning not mentioned here, the heat of the fire itself would seem to be the most likely factor to which the plants could make a flowering response. One possible explanation for this would be the presence of a heat-labile floral inhibitor in the plant. If this chemical resides or is active in the crown of the plant, at or near the soil surface, it would be destroyed by burning. This would allow increased flowering following a fire. The existence of a heat-labile inhibitor is consistent with the

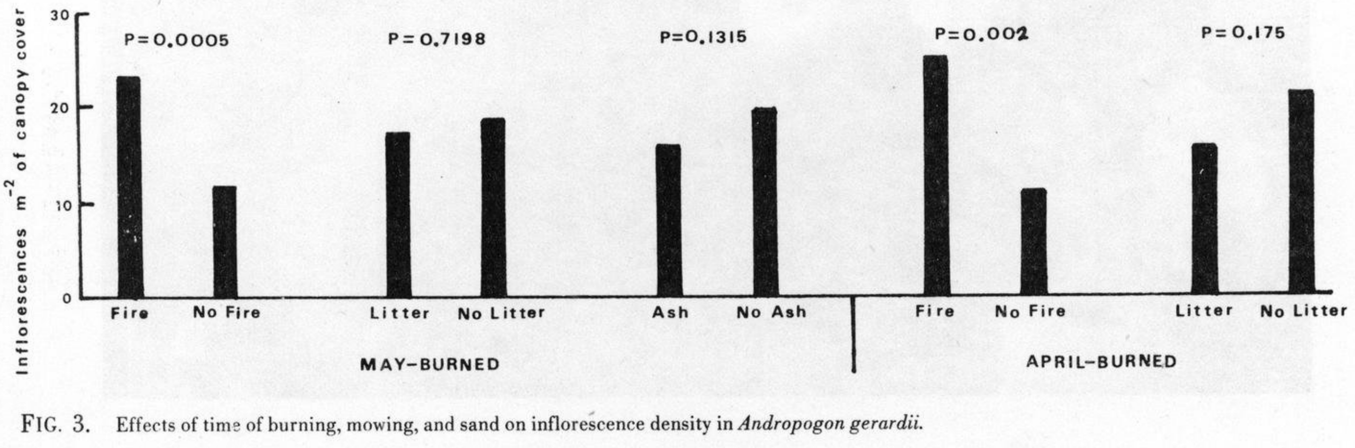

FIG. 3. Effects of time of burning, mowing, and sand on inflorescence density in *Andropogon gerardii*.

observation that flowering does occur but at a lower frequency in the absence of fire (Curtis and Partch 1950, Rice and Parenti 1978). Such an inhibitor may break down with time or simply with an increase in soil temperature but not to the extent to which it is broken down by fire. Thus, litter removal may lead to an increase in flowering, but burning would lead to a much larger increase in flowering in *Andropogon gerardii.*

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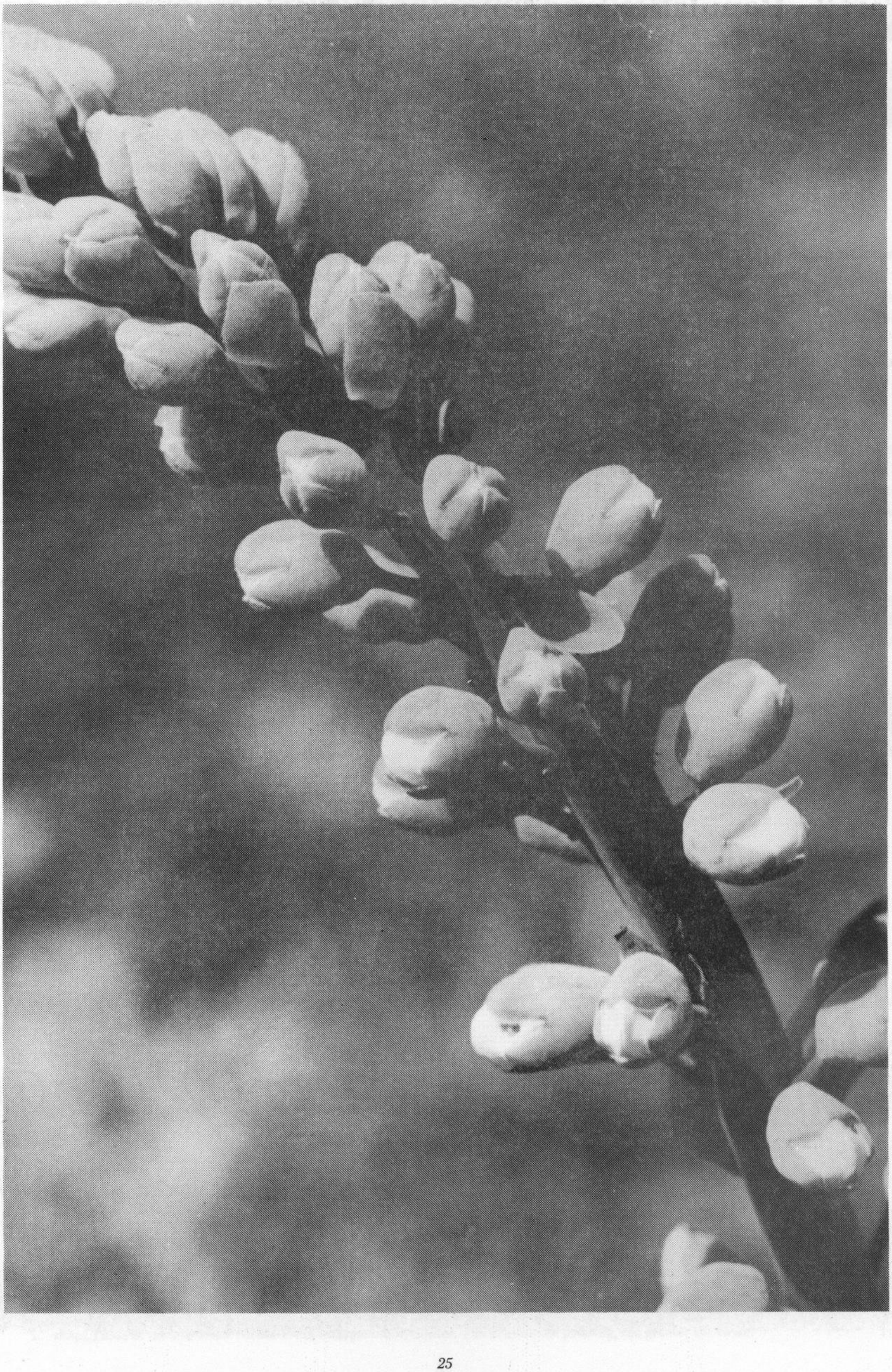
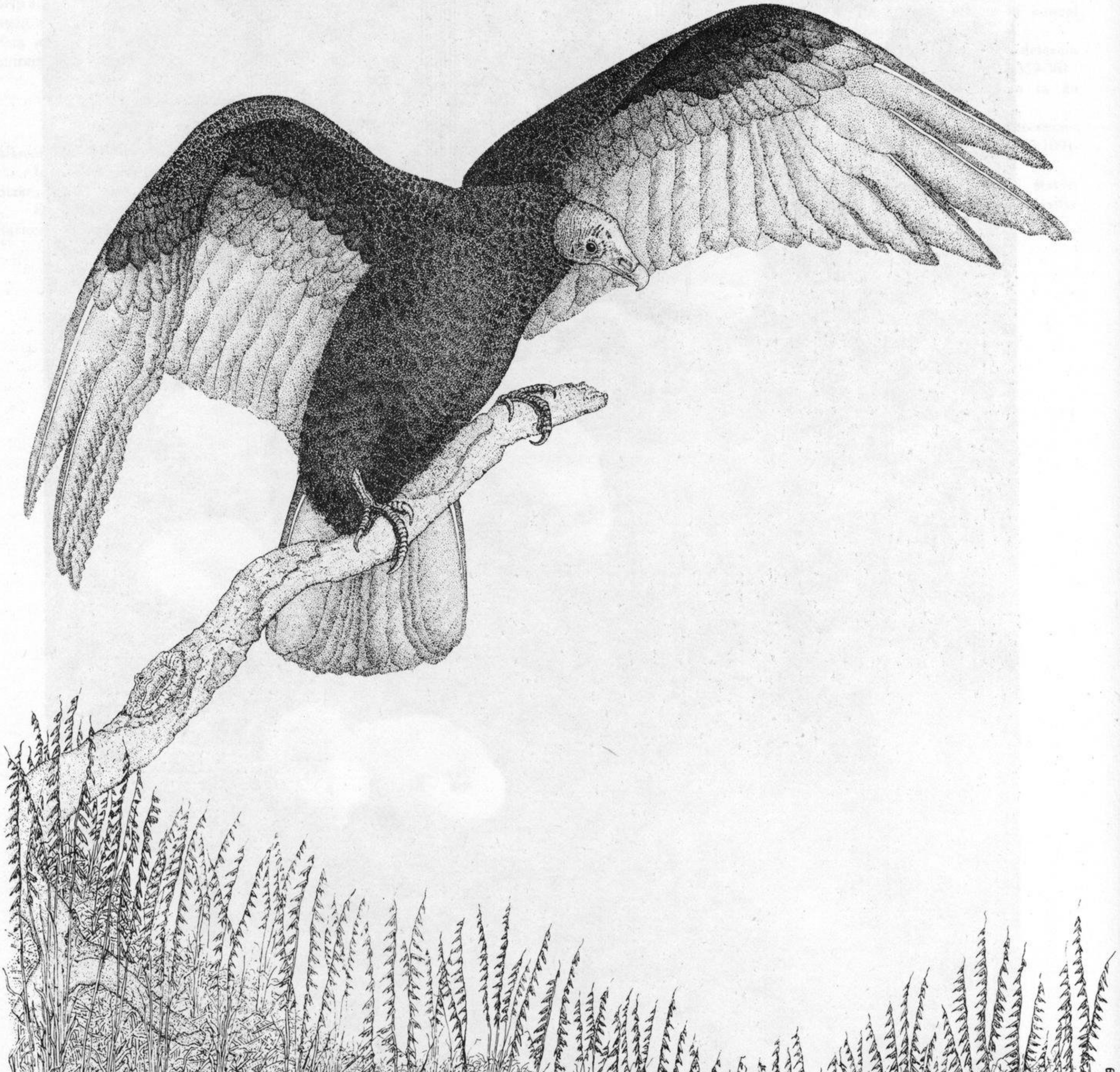


Part 2. Population and Community Ecology



JAMES WOODWORTH PRAIRIE PRESERVE: A CASE HISTORY OF THE ECOLOGICAL MONITORING PROGRAMS

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Abstract. A computer-based analysis using data from 230 1-m² quadrats in the 2.1-ha James Woodworth Prairie Preserve is designed to monitor ecological dynamics and assess effects of prairie management. Output can include computer-generated isopleth maps of such information as species distribution, richness, and an importance value based on frequency and relative cover. This method can provide objective information for management and theoretical studies.

INTRODUCTION

Because of non-standardized methods, available assessments of ecological conditions and land management are of little value in comparing management in different nature preserves. Each manager has unique management goals; consequently, preserve management is usually subjective by nature. A method has been developed for monitoring ecological conditions at the James Woodworth Prairie Preserve that, if widely adopted, would facilitate comparison between different areas and provide a reproducible, reasonably objective method for understanding many components of biological communities and effects of management in preserves.

The method was designed to be (1) standardized and reproducible, (2) objective, (3) able to reflect field situations and management needs accurately, (4) useful in delineating ecological relationships using biologically relevant and statistically significant data, (5) able to guide management when and where management is needed, (6) applicable to other systems, (7) able to handle large volumes of data from intensive field work using reputable methods, (8) useful for assimilation and correlation of different data, (9) serviceable as a baseline for management decisions and reference, and (10) relatively inexpensive to apply.

The Woodworth Prairie Preserve, a 2.1-ha (5.3-acre) remnant tallgrass prairie, is located between Niles and Glenview, Illinois, on the east side of Milwaukee Avenue 0.8 km (0.5 mi.) north of the Golf Road intersection. Purchased in 1968, it has been managed by the University of Illinois at Chicago. It is used for public interpretive programs and scientific study of the prairie ecosystem under its own administration. The area has been used for entomological (Park et al. 1949, 1953; Auerbach 1951; Hamilton 1973; Hamilton and Kuritsky 1981), floristic and other investigations (Paintin 1929; Betz and Cole 1969; Apfelbaum and Rouffa 1981). Over 200 plant species are found in this preserve.

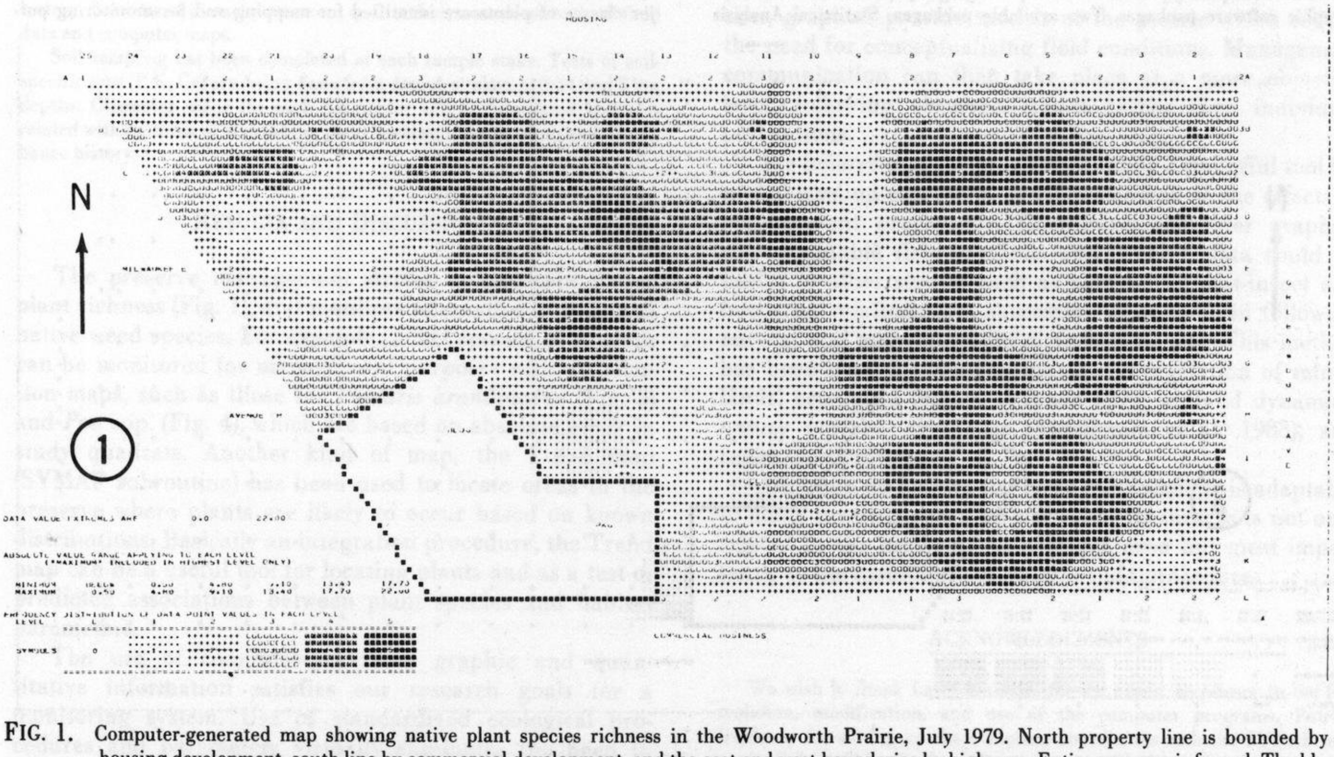

FIG. 1. Computer-generated map showing native plant species richness in the Woodworth Prairie, July 1979. North property line is bounded by a housing development, south line by commercial development, and the east and west boundaries by highways. Entire preserve is fenced. The blank "L"-shaped area in the southwest corner is the Interpretation Center. The heavier the printing, the greater the value.

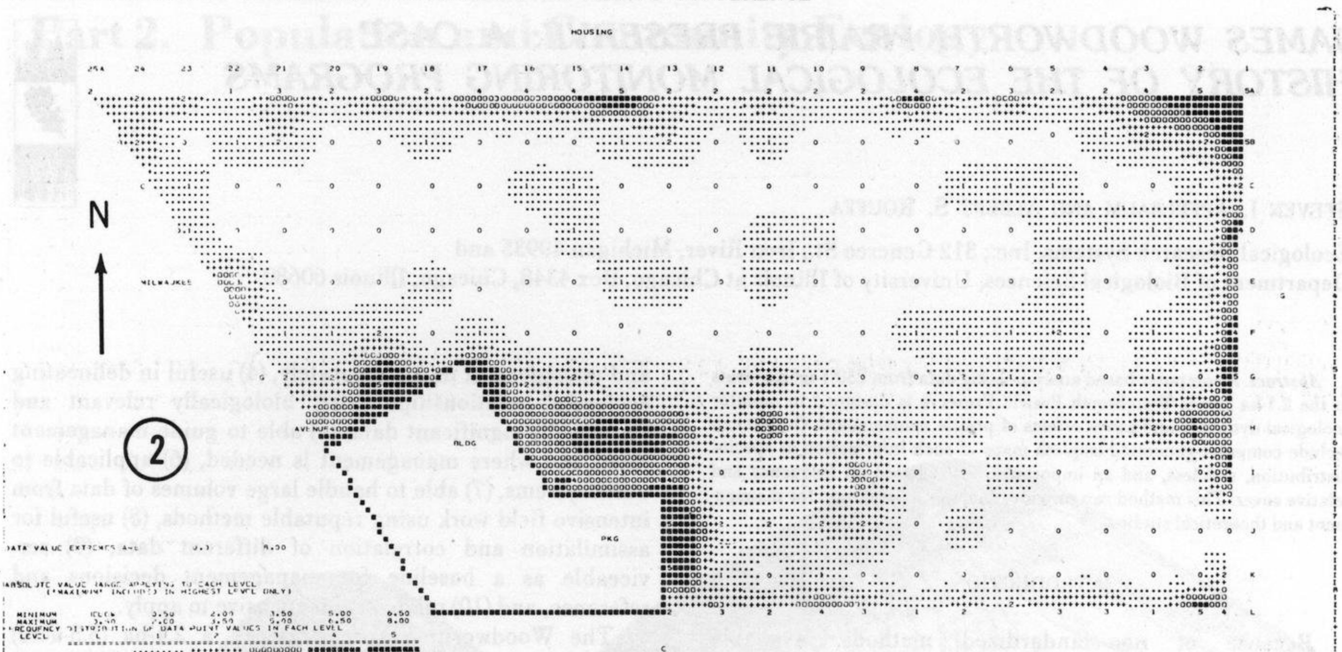

FIG. 2. Computer-generated map showing non-native plant richness, July 1979. The grid of quadrats can be seen best in the blank areas. Compare with Fig. 1.

METHODS

Permanent 1-m² sample quadrats were established along a 10 × 10 m grid system with corner stakes set at each 10 m point. Each stake is the center of a permanent sample quadrat. Sample quadrats (n=230) are located each season for data collection by centering each stake within the confines of a circular 1-m² loop. Four years (1979-1982) of data on plant species richness and absolute % cover for each plant species have been recorded in each quadrat. Absolute cover is estimated to the nearest % (cover-class techniques are not used since they are too subjective). Field data are computer punched and run through various statistical and graphic software packages. Two available packages, Statistical Analysis System, and Harvard University SYMAP have been modified for our use, and coordinate data analysis with numerous software subroutines that we have written. Data entry is accomplished on a portable Osborne microcomputer at the preserve, or wherever convenient, and then sent by modem to the University of Illinois mainframe computer center in Chicago. Analysis is done by the mainframe computer.

Five indices are derived from field data and used for monitoring vegetation dynamics and effects of management. These include (a) relative % species cover, (b) relative % frequency, (c) distribution, (d) an importance value (relative % cover + relative % frequency), (e) patterns of species richness (our measure of spatial heterogeneity). In addition, 3 major classes of plants are identified for mapping and for monitoring pur-

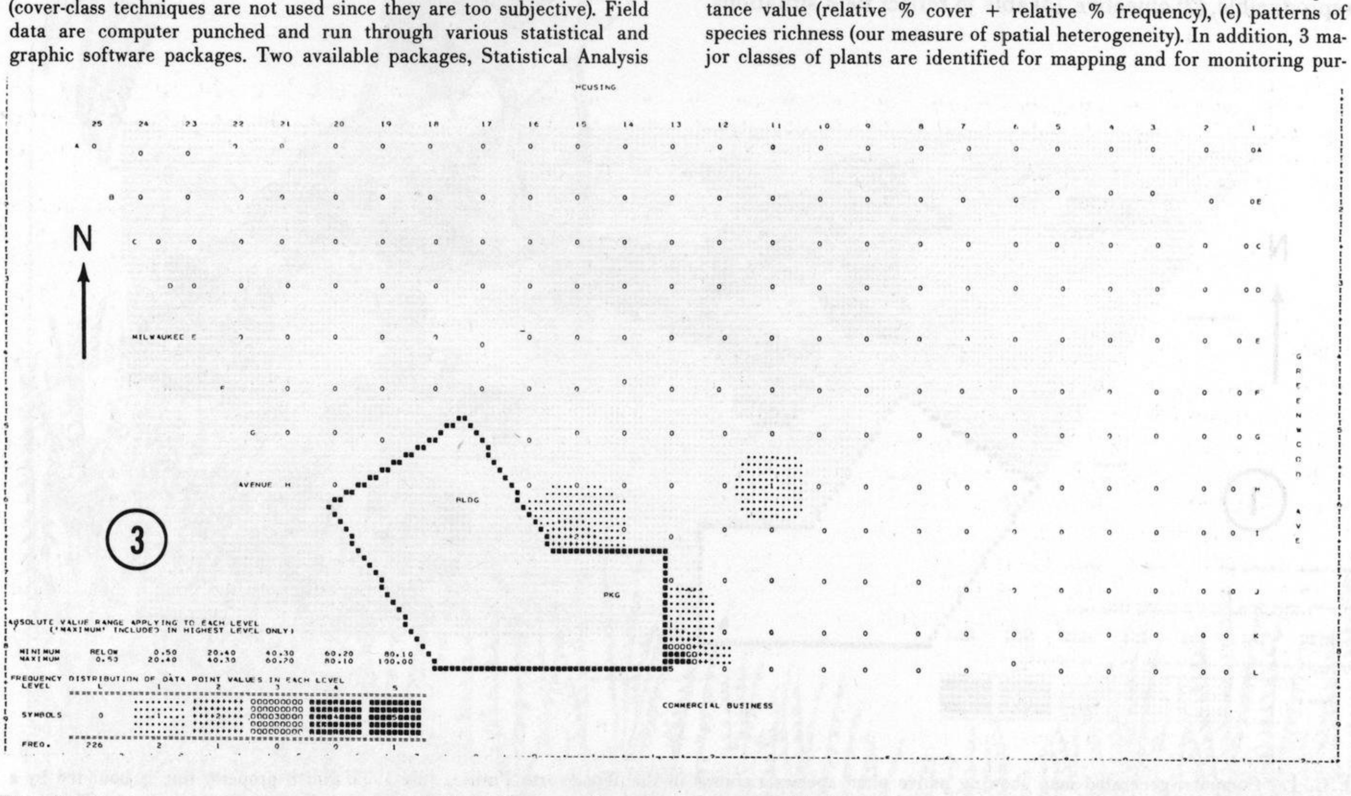

FIG. 3. Computer-generated map showing absolute % cover of reed canary grass (*Phalaris arundinacea*), July 1979. This persistent non-native species is difficult to eradicate once established. Note grid of quadrats in blank areas. See Fig. 1 caption for boundary information.

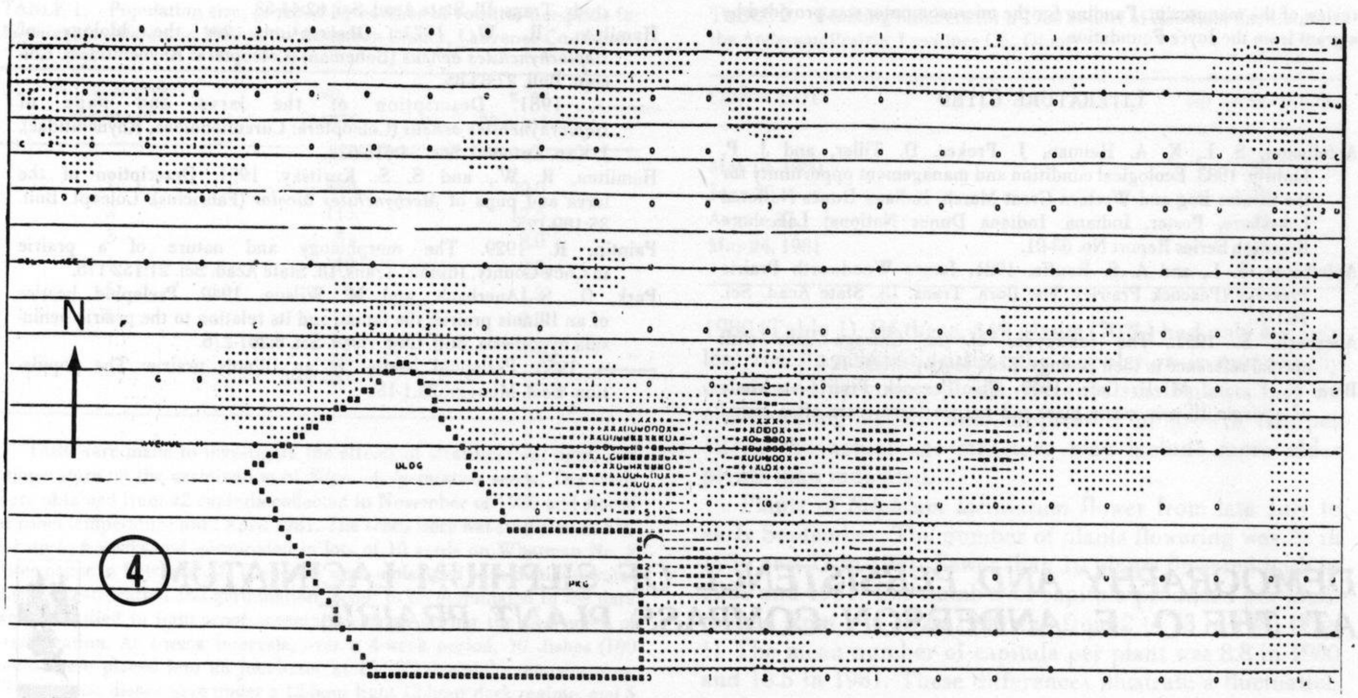

FIG. 4. Computer-generated map of absolute % cover of bluegrass (*Poa* spp.), July ,1979. These non-native grasses persist along fences and other disturbances. See Fig. 1 caption for boundary information.

poses to show relationships with disturbance and management. These include: (1) native plants (desirable prairie species), (2) native weeds (plants that occur in disturbed areas in the prairie, may or may not be indigenous to the prairie, and may be management problems), and (3) non-native plants (naturalized in North America).

Anthropogenic disturbance history has been prepared from archive aerial photographs spanning 1949-1970 (from Chicago Aerial Survey, Des Plaines, Illinois), literature reports, and conversation with local residents. Ownership history, traced to an 1843 land preemption and an 1845 land patent, obtained from the Cook Co. Recorder and Registrar of Titles, Chicago, also proved useful for deciphering land-use and disturbance history. Patterns of disturbances were qualitatively correlated with all field data and computer maps.

Soil sampling has been completed at each sample stake. Tests of soil-specific ions (P,K, Ca) are being done from samples taken at 2.54 and 5 cm depths. Computer maps for each parameter will be generated and correlated with patterns of vegetation, plant species, management, and disturbance history.

RESULTS AND DISCUSSION

The preserve management strives to maintain native plant richness (Fig. 1), and monitors non-native (Fig. 2) and native weed species. For example, select species of concern can be monitored for management purposes with distribution maps, such as those for *Phalaris arundinacea* (Fig. 3) and *Poa* spp. (Fig. 4), which are based on absolute cover in study quadrats. Another kind of map, the Trend map (SYMAP subroutine) has been used to locate areas in the preserve where plants are likely to occur based on known distributions. Basically an integration procedure, the Trend map can be a useful tool for locating plants and as a test of predicted associations between plant species and habitat parameters.

The use of computer-generated graphic and quantitative information satisfies our research goals for a monitoring system. Use of standardized ecological procedures and parameters virtually eliminates the need to assign the subjective and therefore arbitrary "values" or "indices" to any species or group of species often employed by other monitoring methods. Graphics show where sampled species occur based on actual field observation and therefore pinpoint where various management procedures may be necessary. Although the Woodworth Prairie study has used 2 objective field measurements for plants, other characteristics could be selected; examples are productivity and structural aspects. The use of standardized computer programs for preparing maps reduces subjectivity. In addition, graphics provide models of the prairie which reduce the need for conceptualizing field conditions. Management communication can then take place at a more objective level, following observed trends rather than individual perceptions.

We believe that this method could be a powerful tool for understanding ecosystem dynamics as well as the effects of management procedures. Combining computer graphics with reputable field methods and reliable data could be useful in other studies such as monitoring pest-insect and host-crop relationships, succession of vegetation following natural and anthropogenic disturbances, etc. This method has been used (by S.A.) to monitor revegetation of mined lands, ecological effects of forest fires, wetland dynamics, nature preserve dynamics (Apfelbaum et al. 1983), and range land practices.

Although we believe the basic methodology is adaptable to many investigations, we warn that its success is not only related to the hardware or software used but most importantly to the careful use of reliable field procedures.

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DEMOGRAPHY AND PERSISTENCE OF SILPHIUM LACINIATUM AT THE O. E. ANDERSON COMPASS PLANT PRAIRIE

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Abstract. The O. E. Anderson Compass Plant Prairie, located in the forested hill country of unglaciated southeastern Ohio, supports the only known population of *Silphium laciniatum* L. in the state. An investigation of the vegetation at this site and the reproduction of *Silphium laciniatum* was undertaken in 1980 and 1981. The population is concentrated in an area disturbed by soil slippage. The age structure of the population (641 plants) was inferred from relative size. Seventy % of the plants were in the youngest age class. In 1980 the 26 flowering plants had a mean of 8.8 heads per plant, while in 1981, 72 plants flowered and had a mean of 18.5 heads per plant. Seedling survival over 1 year was 98% for a cohort germinating in 1980. Laboratory tests of some effects of temperature and light on germination indicated that cool temperatures (15/5°C) inhibit germination in light but not in the dark. In contrast seed germination percentages were high either in the light or in the dark at 25/15°C.

INTRODUCTION

Much interest in plant demography has been generated among plant ecologists trying to understand the ecological forces which shape plant population structure (Harper 1977) and the evolutionary forces which shape life-history characteristics (Solbrig 1980). Grubb (1977) emphasizes the importance of differences in plant regeneration which contribute to distributional patterns observed at any 1 time, thus distributions of adult plants often reflect the outcomes of events early in their life history (see also Harper 1977, Hamrick 1979, Werner 1979). The persistence of some plant species in communities is a function of disturbance. In general, disturbance creates patchy, transient environments in which succession occurs on a local scale (Platt 1975, Pickett 1980). The only known population of *Silphium laciniatum* in Ohio was studied to determine population size and reproductive aspects in order to get an indication of the potential persistence of the population in view of its rare and disjunct nature.

Prairies in Ohio represent the eastern outliers of the Prairie Peninsula (Transeau 1935) and indicate a past warmer and drier climate (Braun 1928, Sears 1942). The prairies occur primarily in the glaciated portion of the state (Sears 1926, Transeau 1935, Cusick and Troutman 1978); however, the only extant population of *Silphium laciniatum* in Ohio occurs within the unglaciated, forested hill country of southeastern Ohio at the O. E. Anderson Compass Plant Prairie (UTM coordinates 425010mN,371500mE) in Lawrence County (Cusick 1978).

The presettlement vegetation of Lawrence County has been characterized as mostly mixed oak (Gordon 1966). The soils are of the Gilpin-DeKalb association (Ritchie 1973) soil series in Vandalia and are prone to small landslips (Ohio Department of Natural Resources, pers. comm.). A thin bed of Brush Creek limestone of the Conemaugh formation outcrops on the prairie. The site was cultivated in the 1920s, after which it was used for hay and pasture until 1981 (F. W. Darling, pers. comm.).

METHODS

The *Silphium laciniatum* population was sampled to determine its size and aspects of its reproduction. The study extended from April 1980 to August 1981. The number of plants making up the population was determined by a direct count. Age structure was inferred by grouping the plants based on the number of leaf rosettes per plant. In 1980 seedlings of *Silphium laciniatum* were mostly found concentrated in 2 localities, thus 2 permanent 1 m² quadrats were placed in these localities for the determination of seedling survival. Seedlings were censused on 18 May, 29 June, and 27 August in 1980 and on 24 May in 1981.

The number of plants flowering and the number of capitula per plant were noted for the entire population in both 1980 and 1981. Ten capitula, 1 on each of 10 plants, were bagged prior to anthesis.

TABLE 1. Population size, grouped by number of rosettes per plant for *Silphium laciniatum* in 1980 at the Anderson Prairie, Lawrence Co., Ohio.

No. ROSETTES PER PLANT	No. PLANTS	% OF POPULATION
1	449	70.0
2	113	17.6
3	51	8.0
4	18	2.8
5	8	1.2
6	1	0.2
7	1	0.2
	Sum 641	

Tests were made to investigate the effects of stratification, light, and temperature on the germination of *Silphium laciniatum* seeds. The seeds were obtained from 42 capitula collected in November of 1980 and stored at room temperature until April 1981. The seeds were wet-stratified at 5°C for up to 6 weeks and germinated in lots of 10 seeds on Whatman No. 2 filter paper in Petri dishes. The seeds were moistened with distilled water during stratification and germination. Seeds to be germinated in the dark were stratified in light-proof containers except during the first week of stratification. At 1-week intervals, over a 4-week period, 10 dishes (100 seeds) were placed into an incubator at 15/5°C day/night temperatures. Five of these dishes were under a 12-hour light 12-hour dark regime, and 5 were in 24-hour darkness. Final counts of germinated seeds were made after 30 days. Germination was scored as radicle emergence. A group of 173 stratified seeds were germinated in light and dark at 25/15°C temperatures, to examine the effect of warm temperatures on germination. Final counts were made after 7 days. Student's *t*-tests were used to analyze the data.

RESULTS AND DISCUSSION

The *Silphium laciniatum* population at the Anderson Prairie is distributed in an area with evidence of recent soil slippage, and also along an intermittent stream which drains the site. The population consisted of 641 plants in 1980 (Table 1). Of these, 449 plants (70%) had only a single leaf rosette suggesting that the population is numerically dominated by young plants. Because small plants may be either young or old and suppressed in growth (Harper 1977), the actual age structure may include more older plants than indicated.

TABLE 2. Seedling numbers for a 1980 cohort of *Silphium laciniatum* at the Anderson Prairie, Lawrence Co., Ohio.

CENSUS DATE	NO. OF SEEDLINGS
May 18, 1980	50
June 29	42
August 27	43
May 24, 1981	49

Plants of *Silphium laciniatum* flower from late July to early September. The number of plants flowering was 26 in 1980 and 72 in 1981. Fewer than 10 plants flowered both in 1980 and 1981. The number of capitula produced per plant ranged from 1 to 49 in 1980 and from 2 to 73 in 1981 (Fig. 1). The mean number of capitula per plant was 8.8 in 1980 and 18.5 in 1981. These differences illustrate a fluctuation in the reproductive structure of the population between years. There is an increase in both the proportion of the population reproducing and in the mean number of capitula per plant. One result of this annual variation will be pulsed inputs to the seed bank (see Rabinowitz 1981). Because few plants in this population flower in consecutive years, it is likely that flowering depends on the accumulation of some threshold level of food reserves, as suggested

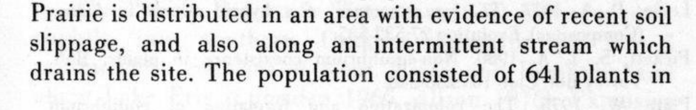

FIG. 1. Number of flowering individuals of *Silphium laciniatum* in capitula number classes in 1980 and 1981.

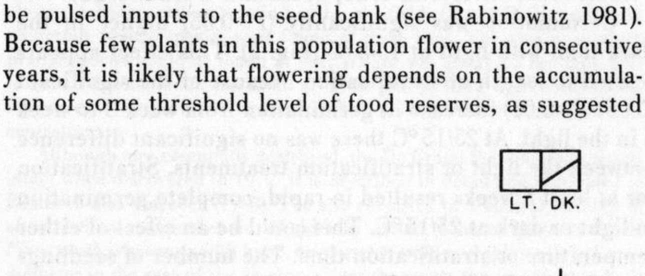

FIG. 2. Percent germination after 1-6 weeks of stratification with 12 hr. light and in the dark, at 15/5°C (30 days) and 25/15°C (7 days). Error bars represent standard deviations.

for *Liatris* spp. by Levin (1973) and Roberts et al. (1977). The bagged capitula did not set seed, suggesting that *Silphium laciniatum* is either self-incompatible or non-autogamous. A variety of insects were observed on open capitula, including Diptera, Hymenoptera, and Coleoptera.

Silphium laciniatum seeds germinated in May. In 1980, an initial cohort of 50 seedlings appeared to decline to 42 between 18 May and 29 June, as indicated by leaf senescence (Table 2). However, in the spring of 1981 it became clear that most of the seedlings had actually survived. Thus leaf senescence is not a reliable indicator of seedling mortality in this species; consequently, only those seedlings marked at germination that did not reappear in the following year were presumed dead. Survivorship was 98% for the plants observed from May 1980 to May 1981. Such high survivorship is unusual. Silvertown and Dickie (1980) noted less than 20% survival for 9 herbaceous perennials of English chalk grasslands. Harper (1977) also cites studies with herbaceous perennials in which survivorship was generally 20% or less. Grubb (1977) points out that seedling mortality most likely varies with environmental conditions at the time of establishment, being important in some years but not in others. The high survivorship may be influenced by soil slippage since the establishment of new individuals in populations is frequently coincident with some form of disturbance (Cook 1979) and since patchy openings are an important component of plant establishment (Platt 1975, Pickett 1980, Silvertown 1981, Gross and Werner 1982).

Germination was significantly ($P>0.05$) higher in the dark than with light at 15/5°C (Fig. 2). This effect appears related to length of stratification because of the significant ($0.05>P>0.01$) increase in germination from week 3 to week 4 in the light. At 25/15°C there was no significant difference between the light or stratification treatments. Stratification for at least 5 weeks resulted in rapid, complete germination in light or dark at 25/15°C. This could be an effect of either temperature or stratification time. The number of seedlings observed in the field indicate that only a small percentage of each year's seeds germinate the next year. This could be due to rodent and fungal predation or to induced dormancy. Burial induces a light requirement for germination in seeds of English pasture species (Wesson and Wareing 1969). Seed dormancy in such species can also be induced by a grass canopy (Silvertown 1980) or hardwood leaf litter (King 1975). If there is induced dormancy in *Silphium laciniatum* then disturbance may be essential for seed germination, even though seeds initially germinate in complete darkness.

This population of *Silphium laciniatum* is distributed in and around the area of soil slippage. The population appears dominated by young plants and seedling survivorship is high, indicating that successful reproduction is occurring. Because of the role of disturbance in plant establishment and since it is generally believed that prairie perennials are long-lived (Werner 1978) it is likely that this population will continue to persist and that its persistence is related to soil slippage.

ACKNOWLEDGMENTS

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ASSOCIATION OF RELICT PRAIRIE FLORA WITH INDIAN TRAILS IN CENTRAL ONTARIO

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Abstract. Near Georgian Bay in central Ontario, 4 small areas were discovered that had a distinctive prairie flora. Two of the areas had remnants of prairie vegetation intact, but the integrity of the other communities had been destroyed, though the flora still persisted along roadsides and railway tracks. Because of the presence of prairie species, the sites were of great local floristic interest, containing many species found nowhere else in the region. Formerly, the sites were important stopping places on Indian and early voyageur routes between Lakes Ontario and Huron. In addition, historical documents describe open space there beginning with the earliest records. One of the sites was visited by John Goldie in 1819, and he recorded the prairie species *Ranunculus rhomboideus* (type locality), *Asclepias tuberosa*, and *Euphorbia corollata*. All sites were sandy, ± flat terraces at the base of Algonquin-age beach bluffs. Searches have found no similar assemblages elsewhere in the region. It is hypothesized that these sites are remnants of prairie-like communities widespread on the shores of the postglacial Great Lakes during the Hypsithermal Interval. Even then, Indian portage routes would presumably have been established and these sites would have been important camping areas, as they were only 180 years ago. With the recession of the lakes and a slightly cooler, moister climate approaching the present, all of these communities except those kept continuously open by Indian occupation became forested.

INTRODUCTION

The Prairie Peninsula (Transeau 1935) extended only slightly into southern Ontario, primarily in the 3 southwestern counties of Kent, Essex and Lambton, and along Lake Erie (Lumsden 1966, Alison 1976). Extensive areas of prairie are still known in this area (Rogers 1966, Thompson 1975). Farther east and north, prairie flora and vegetation occurred as scattered remnants on hill crests, steep south-facing banks, etc. Most of these sites have now been destroyed through successional changes, intensive grazing, and urban development. However, even in those areas where the integrity of the vegetation has been destroyed, depauperate remnants of the flora often persist along nearby railways, roadsides, and in adjacent abandoned fields.

Of particular interest here are 4 of the northernmost areas of prairie flora and vegetation in southern and central Ontario, located in the Georgian Bay region. The 4 are located, from south to north (Fig. 1), near the town of Holland Landing, at De Grassi Point on Cooks Bay, Lake Simcoe; along Kempenfeldt Bay, Lake Simcoe at Barrie; and near the village of Minesing at the site of the historic Fort Willow. Exact locations are: Holland Landing—York County, East Gwillimbury Township, Concession Iw, lot 11'-115, about 2.4 km NNW of Holland Landing, 44°07′ N, 79°30′ W; De Grassi Point—Simcoe County, Innisfil Township, Concession II, lot 24, 19 km SE of Barrie, 44°15′ N, 79°30′ W; Kempenfeldt Bay—Simcoe County, Barrie, about 2 km W of center of City along shore of Kempenfeldt Bay, 44°23′ N, 79°40′ W; Fort Willow—Simcoe County, Vespra Township, Concession XI, lot 14, 5.6 km S of Minesing, 44°23′ N, 79°49′ W. Extensive work in the Georgian Bay region has disclosed only these 4 sites with a distinctive prairie flora.

The objective of this paper is to give floristic and vegetation data about these 4 prairie areas, demonstrate that an open, presumably prairie-like vegetation existed at these sites before settlement by European man, and present a hypothesis explaining the origin of this vegetation.

VEGETATION

Although all 4 sites had a prairie flora, they differed considerably in vegetation. Two, Fort Willow and Kempenfeldt Bay, had no original prairie vegetation intact, although occasional areas dominated by stands of *Andropogon gerardii*, *A. scoparius* and *Sorghastrum nutans* occurred along roadsides, railways or in nearby old fields (Fig. 2-5). Nevertheless, numerous prairie species were found at these sites. The area over which prairie species could be found at Fort Willow was about 3-5 hectares. Due to urban development, the small areas of prairie flora were quite widely scattered in the Barrie area, and Fig. 1 shows only the area of major concentration.

Although now essentially destroyed, the De Grassi Point site was nearly intact when discovered in 1972. It is described in detail and illustrated in Reznicek and Maycock (1983). The site consisted of a central opening of about 1.6 ha surrounded on all sides by about 11 ha of *Quercus rubra*-*Pinus strobus* savanna with huge, open-grown trees averaging nearly 1 m in diameter in the case of the *Quercus*. Near the water, the savanna was built up with cottages, although many of the savanna trees were left. Elsewhere, it was intact although the understory was mostly overgrown by dense saplings and shrubs. The prairie opening was on a very gentle slope. The driest areas were dominated by *Andropogon scoparius* accompanied by *Solidago nemoralis, Danthonia spicata, Sorghastrum nutans* and *Aster azureus*. In the lowest, mesic to wet-mesic (Curtis 1959) areas, the dominants were *Sorghastrum nutans* and *Desmodium canadense* accompanied by *Equisetum hyemale, Aster sagittifolius* and *A. azureus*.

The prairie opening was rich with 120 species (including 5 historical records). Over ⅓ were prevalent or modal prairie species, based on lists of prairie and related communities in Curtis (1959) (Reznicek and Maycock 1983).

Although heavily damaged by agricultural and residential development, the Holland Landing site was the largest and floristically richest of all the sites. Here, prairie species were scattered irregularly over several hundred hectares. A few small sites, on the driest soils within this large area, had good prairie vegetation dominated by *Andropogon gerardii* with *Andropogon scoparius, Danthonia spicata, Ceanothus americanus* and *Carex foenea.* The site and its vegetation are described and illustrated in Reznicek (1980).

Only at De Grassi Point was the prairie opening surrounded by a savanna of old open-grown trees. However, at the other sites, occasional large, open-grown *Quercus rubra* were seen along fencerows and roadsides, and it is likely that all sites originally had a similar structure.

At De Grassi Point, the soils of the prairie opening were examined in some detail (Reznicek and Maycock 1983). All areas of rich prairie vegetation showed a marked accumulation of humus in the soil, a lack of horizon differentiation and a calcareous *p*H. These features indicate long occupation by grassland vegetation, rather than mixed forests typical of the region.

FLORISTICS

As might be expected, these tiny islands of prairie flora contained many species that are rare in the region. Table 1 lists for all 4 sites the species of prairie affinity that are of restricted distribution in the Georgian Bay region. Not included are common species of prairies such as *Fragaria virginiana, Achillea millefolium,* etc. (Curtis 1959) that occur in so many plant communities that they mean little in terms of floristic affinities. Although most of the species in Table 1 are uncommon to very rare in the region, a few characteristic prairie species are more or less widespread on sand dunes and rocky barrens. In addition, there are, of course, some regionally rare species at these sites that are not of prairie affinity. However, comparison of the Holland Landing list in Table 1 with the complete list of regionally rare species presented in Reznicek (1980) shows that the great majority of the rare species are indeed of prairie affinity. There is a consistent core of species present at all sites, including the major dominants *Andropogon gerardii, A. scoparius* (absent at Kempenfeldt Bay), *Sorghastrum nutans, Desmodium canadense, Cyperus filiculmis, Carex muhlenbergii, C. richardsonii* and *Anemone cylindrica.* However, each site has a somewhat different set of species, and all but the Fort Willow site have unique species.

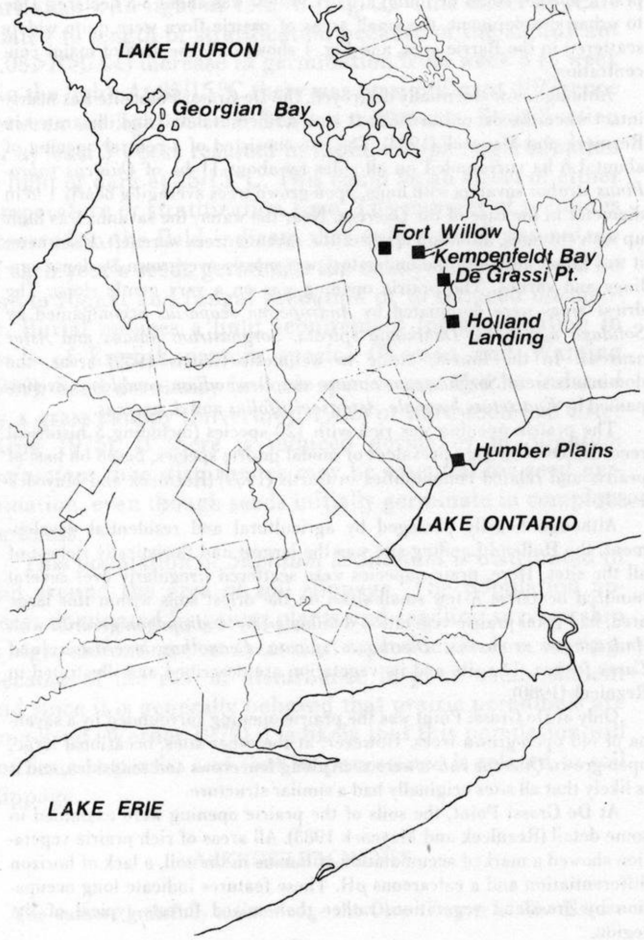

FIG. 1. Location of prairie relict areas in central Ontario.

TABLE 1. Species of prairie affinity occurring at Holland Landing, DeGrassi Point, Kempenfeldt Bay and Fort Willow that are of restricted distribution regionally. X = collections in MICH, TRT or TRTE; S = sight record only.

	Location			
Species	Holland Landing	DeGrassi Point	Kempenfeldt Bay	Fort Willow
Bromus kalmii	X	X*	X	X
Elymus canadensis	—	X*	X	S
Sporobolus cryptandrus	X	S	X	X
Panicum virgatum	—	—	X	—
Panicum oligosanthes	—	—	X	—
Panicum praecocius	X	—	—	—
Andropogon scoparius	X	X	—	X
Andropogon gerardii	X	X	X	X
Sorghastrum nutans	X	X	X	X
Cyperus filiculmis	X	X	X	X
Cyperus houghtonii	X	—	X	X
Scirpus clintonii	—	X	—	—
Carex foenea	X	—	—	—
Carex muhlenbergii	X	X	S	S
Carex richardsonii	X	X	X	X
Zigadenus glaucus	X	—	—	—
Corylus americana	X	—	—	—
Ranunculus rhomboideus	X	S*	—	—
Anemone cylindrica	S	S	S	S
Arabis divaricarpa	—	X	—	—
Arabis holboellii	—	—	X	X
Amelanchier alnifolia	X	—	—	—
Prunus besseyi	X	—	—	—
Desmodium canadense	X	X	X	S
Desmodium dillenii	—	—	X	—
Desmodium paniculatum	—	—	X	X
Lespedeza intermedia	—	X	X	—
Lespedeza capitata	—	X	X	—
Polygala senega	—	—	X	—
Euphorbia corollata	X	—	—	—
Ceanothus americanus	X	—	X	X
Ceanothus herbaceus	X	—	—	—
Helianthemum bicknellii	X	—	X	—
Helianthemum canadense	X	—	X	—
Lechea intermedia	X	X	X	X
Viola fimbriatula	X	—	X	—
Gentiana quinquefolia	—	S*	—	—
Asclepias tuberosa	S	S*	S	—
Pycnanthemum virginianum	—	X	—	—
Houstonia longifolia	S	S	S	X
Campanula rotundifolia	X	X	—	—
Helianthus strumosus	—	X*	X	—
Helianthus rigidus	X	—	—	—
Aster azureus	—	X	—	—
Aster laevis	X	—	—	—
Erigeron pulchellus	—	X	—	—
Cirsium discolor	—	X*	—	—
Total species = 47	30	26	27	17

* historical record only

The regional floristic significance of these sites can be seen from the fact that 11 (Table 2) of the 47 species (23%) listed in Table 1 are known in the Georgian Bay region only from 1 or more of these 4 sites. For most of these species, occurrence here represents a significant disjunction (Reznicek 1980), sometimes of hundreds of kilometers.

HISTORICAL SIGNIFICANCE AND EVIDENCE OF PRAIRIE

In addition to being the only sites where this type of prairie flora occurs in the Georgian Bay region, these 4 sites have other historical features in common. Georgian Bay extends deep into this part of Ontario (Fig. 1) and combined with Lake Simcoe and associated rivers, produces a water route from Lake Ontario to Lake Huron with only 2 stretches where overland travel is necessary. This route was well used historically. One of the 2 overland portions was the famous Nine-Mile Portage, renowned during the War of 1812. It ran from the north side of Kempenfeldt Bay at Barrie to the site of old Fort Willow, an important depot in the War of 1812 (Hunter 1948). This portage was expanded to a wagon road in 1815 (Laidler 1943, Jury and Jury 1956), but was a well-known Indian trail previous to this. Head (1829: 300-302) gives an eye-witness description of Indian portaging along this trail and Jury and Jury (1956) note Indian artifacts along the route. The other trail, a long one of 37 miles, ran from Toronto near the mouth of the Humber River[1] to the Holland River just north of the town of Holland Landing (Adam 1885, Lizars 1913, Hunter 1948). This trail was marked as an Indian portage on a number of historic maps—see Lizars (1913, maps facing pp. 20 and 23) for maps dated 1680 and 1689. The correspondence between the landing and departure areas of these portages and the present-day areas of prairie is, allowing for urban development at Barrie, exact for all but the De Grassi Point site. De Grassi Point, although not a terminus of a portage trail, was the first sandy, flat, dry landing on Lake Simcoe after 1 departed from Holland Landing and, like the other sites, was a favorite stopping place and rendezvous point for Indians and later, voyageurs and fur traders (Macdonell 1891; Hunter 1893, 1948; Williams 1906). Here, in 1793, Governor John Graves Simcoe briefly visited his friend the Indian chief Canise (Keenees) who was camped here during his terminal illness (Hunter 1893, Macdonell 1891). This route was well-travelled by the Indians when European man first came to the continent, and was followed by early explorers of interior North America, including such famous travellers as La Salle, Alexander Henry, Sir John Franklin, and John Galt. Even people familiar to botanists such as Sir John Richardson (commemorated in *Carex richardsonii,* although he discovered it in the prairie provinces rather than at one of these 4 areas) and John Goldie passed over all or parts of this route.

For all these places except the Kempenfeldt site, there is some historical evidence that open grassland vegetation occupied the sites before extensive clearing by European man. In fact, the Holland Landing site was quite famous and mentioned in travellers' diaries too frequently to quote here. All accounts mention large open areas where Indians converged from great distances to meet and trade. Hunter (1948, pt. 2, p. 3), summarizing many accounts, notes that

> The *open space* referred to by Galt and other early writers was used as a camping-ground by the early Indians and fur-traders. Here could be seen encamped at all seasons of the year large numbers of Indians, often from very remote districts of the upper lakes. . . . On one occasion the writer's grandfather counted no less than thirty wigwams of the larger kind clustered on the *common* adjoining the Landing (italics mine).

John Galt visited the site in 1827, before any extensive European settlement in this part of the country.

Accurate botanical data come from an earlier visit, in 1819, by the botanical explorer John Goldie. Goldie reported from this very site 3 prairie species, *Asclepias tuberosa, Euphorbia corollata* and *Ranunculus rhomboideus* (Goldie 1822, 1897; Spawn 1967; Reznicek 1980) and described their habitat as "dry, sandy fields." In fact, the type locality of *Ranunculus rhomboideus,* described by Goldie, is at Holland Landing. All 3 species reported by Goldie are still present at the site. There can be no doubt that prairie vegetation existed in the "open space" at Holland Landing in the early 1800's.

De Grassi Point, before the mid-1800's, was named Grass (or Grasses) or Grassy Point because

> of there being four or five acres of ground covered with grass extending to the water's edge . . . this special feature of the place was well-known, as it was the rendezvous of fur traders and voyageurs passing up and down Lake Simcoe, this being then the chief route to the almost unknown and impenetrable North-West (Williams 1906).

Of course, the soils and the ancient open-grown oaks, the largest being more than 1.2 m in diameter, also attest to the presence of open grassland at De Grassi Point before European settlement.

There is surprisingly little information about the Kempenfeldt Bay site at Barrie before the area was settled. The site was well-known because it was 1 end of the portage to Willow Creek (the Nine-Mile Portage to Fort Willow) but the person who built the first house at Barrie in 1815, Sir George Head, left no descriptions of the vegetation (Head 1829). Mention of tall, rank grasses in the fall invading new clearings (Hunter 1893: 44) may suggest prairie species.

Very little information exists about the site and vegetation at Fort Willow, since its importance was very short-lived. Hunter (1948, pt. 1, p. 83) notes that "there had been 3 or 4 acres cleared just around the fort and this laid in a common down nearly to the present time."

TABLE 2. Species of prairie affinity known regionally only from Holland Landing, De Grassi Point, Kempenfeldt Bay or Fort Willow.

Panicum oligosanthes
Scirpus clintonii
Carex richardsonii
Corylus americana
Lespedeza intermedia
Euphorbia corollata
Helianthemum bicknellii
Panicum praecocius
Gentiana quinquefolia
Prunus besseyi
Cirsium discolor

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[1] At the mouth of the Humber River there occurred a famous prairie area with many rare species, the Humber Plains—see Lizars (1915: 138). Although not considered here, this area is probably part of the same phenomenon discussed herein.

FIG. 2-3. Above (2)—Fort Willow, tiny area of disturbed prairie dominated by *Andropogon gerardii*, *Sorghastrum nutans*, *Andropogon scoparius* and *Ceanothus americanus* and being shaded out by *Populus grandidentata*, *Quercus borealis* and *Pinus* spp. Below (3)—Fort Willow, dense stand of *Andropogon scoparius* along roadside.

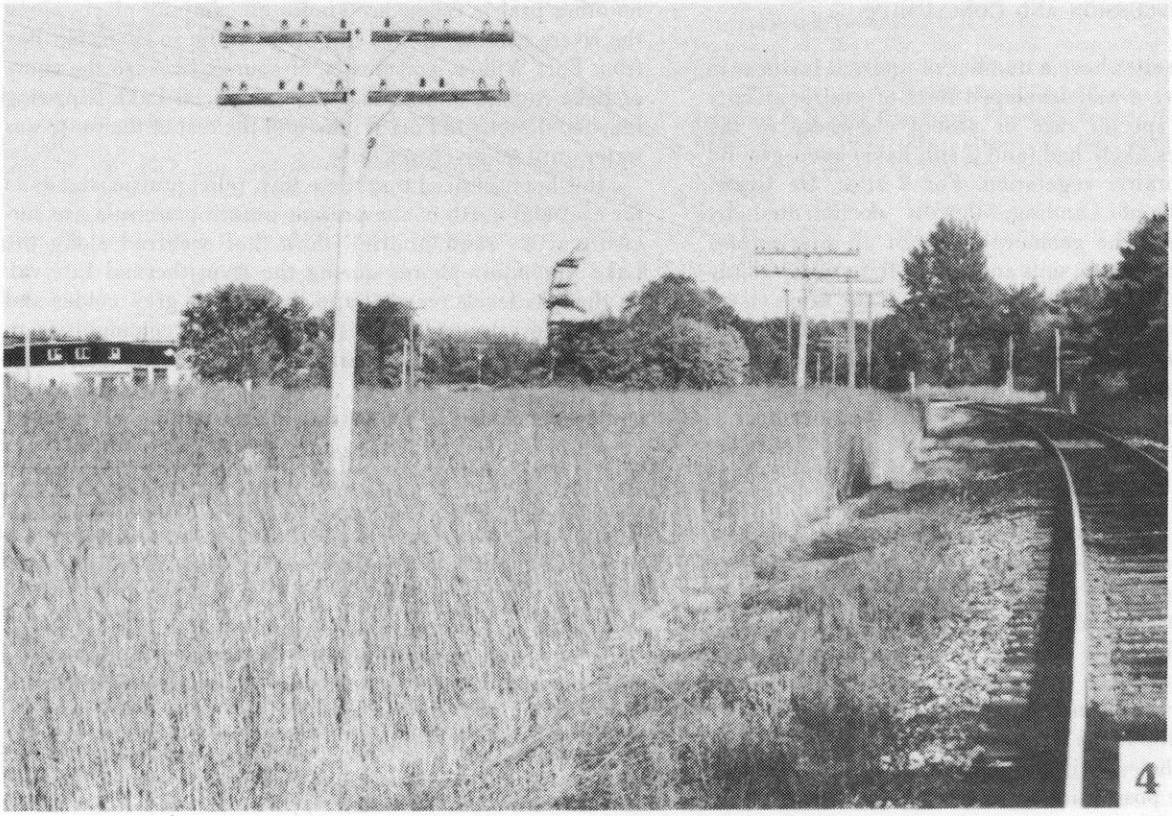

FIG. 4-5. Above (4)—Kempenfeldt Bay, disturbed prairie along railway, dominated by *Andropogon gerardii*, *Sorghastrum nutans*. Below (5)—Kempenfeldt Bay, 0.5-hectare stand of *Andropogon gerardii* in old field.

DISCUSSION AND CONCLUSIONS

All 4 of these sites have a number of unusual features in common. All have a well-developed flora of prairie affinity with numerous species rare or absent elsewhere in the region. All 4 sites likely had (and 2 still have) open ground dominated by prairie vegetation. For 2 sites, De Grassi Point and Holland Landing, this is documented by historical records. The geomorphology of all sites is also similar. All had dry sandy soils and are on flat or very gently rolling small sand plains. The sites occur at the same elevation, 220 m above sea level, and all are situated at the foot of the Lake Algonquin-age beach bluff so pronounced in the Georgian Bay area (Chapman and Putnam 1966). This observation strongly suggests that all were beaches during receding levels of Lake Algonquin. Also, all of the sites were stopping places or termini of portages on a major Indian route.

The richness of the flora, the small size of the area, and the historical records, especially for Holland Landing, establish that these tiny prairie islands are relicts. It is inconceivable that so many species forming such an integrated floristic unit could have been introduced subsequent to European man's clearing of the land—and then only to these few, small areas. Because of the diversity of the flora and the rarity and obscure, tiny nature of some of the species, wholesale introduction by Indians is also rejected as a viable possibility. It is certainly possible that the disjunct colonies of a few species of obvious utility to man such as the hazel (*Corylus americana*), bush cherry (*Prunus besseyi*), and shadbush (*Amelanchier alnifolia* var. *alnifolia*) may have resulted from Indian introduction. Likewise, this possibility also exists for taxa with clinging fruits such as *Desmodium* spp. However, for the great majority of species, and especially insignificant, rare species such as *Scirpus clintonii, Carex richardsonii* or *Ranunculus rhomboideus,* another explanation must be postulated.

During the Hypsithermal Interval, 4000 to 8000 years ago (Deevey and Flint 1957), there was a great eastward extension of the prairie peninsula (Schmidt 1938, Smith 1957, Wright 1968). Although direct evidence is lacking, there very likely was also a more diverse prairie flora associated with the extensive beaches and dunes of Lake Algonquin (whose receding stages may have overlapped in time with the Hypsithermal) than of the present shores of the Great Lakes in the Georgian Bay region. Present-day beaches and dunes of the Great Lakes in areas near the prairie peninsula have a rich component of prairie species, including many found at these 4 prairie sites but not found now on Great Lakes dunes and beaches of the Georgian Bay area (Peattie 1930). Included are species such as *Euphorbia corollata, Lespedeza* spp., and *Carex richardsonii,* among others.

During the Hypsithermal, the Georgian Bay and the western Lake Ontario region were also inhabited by Indians. Although very little is known about the Paleo-Indian (9000-5000 BC) and the Laurentian Archaic inhabitants (5000-1000 BC), the same trails and rendezvous areas would likely have been used then as were found in use by the early explorers hardly more than 150 years ago, since these trails are dictated by the terrain and lakeshore and river configurations. In fact, all the sites discussed here would have been more suitable in the past since they would have been near the water's edge rather than well away from it. Indeed, no other prairie relicts are known on camping places along the rivers making up the rest of the route to Georgian Bay from Fort Willow, and this is, of course, because the shore of Lake Algonquin and also that of glacial Lake Nipissing reached directly to Fort Willow and the rest of the route was water until relatively recently.

It is hypothesized that these tiny, relict prairie islands so far east and north of the present prairie peninsula are survivors of a "sand prairie" flora that occurred along the Lake Algonquin shores during the Hypsithermal Interval. As the lake levels receded and the climate grew colder and moister, forests would have succeeded open communities on these shores, since there was no longer active dune and beach formation. However, at the time of first European contact, those areas that were used for camping and rendezvous sites by Indians were open, presumably kept this way by fire (Day 1953) or perhaps even purposeful clearing of saplings and tree seedlings. Although there were Indian villages and camping sites all through the Georgian Bay region (Hunter 1948), in most cases, these were not continuously occupied (Konrad 1975). The 4 areas discussed here were on such an important route that it is probable that their use was continuous. In these camping areas, hypothesized to have been *continually* used from the time of Lake Algonquin until extensive European settlement, a prairie flora was maintained until the present.

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RESPONSES OF NESTING WILDLIFE TO PRAIRIE GRASS MANAGEMENT ON PRAIRIE CHICKEN SANCTUARIES IN ILLINOIS[1]

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Abstract. A total of 265 ha of seeded (218 ha) and naturally restored (47 ha) prairie grasses was systematically searched on foot for bird and mammal nests on sanctuaries for greater prairie chickens (*Tympanuchus cupido*) from 1967 through 1981. Fields seeded to mixed stands of switchgrass (*Panicum virgatum*), Indiangrass (*Sorghastrum nutans*), and big bluestem (*Andropogon gerardii*) provided suitable nest cover for prairie chickens when high-mowed (> 30 cm) during the late summer or fall prior to a nesting season. Prairie grasses undisturbed or hayed prior to a nesting season showed low rates of nest establishment and nest success for prairie chickens. Nest success by prairie chickens was negatively related to the degree of nest concealment by prairie grasses. There were no significant differences in the rates of nest establishment for either pheasants (*Phasianus colchicus*) or bobwhites (*Colinus virginianus*) among undisturbed, high-mowed, or hayed prairie grasses. The red-winged blackbird (*Angelaius phoeniceus*) was the most common nesting bird in prairie grass fields. Nests of small mammals (*Microtus ochrogaster* and *Synaptomys cooperi*) and cottontail rabbits (*Sylvilagus floridanus*) were most abundant in prairie grasses left undisturbed. In recently burned prairie grass, no nests by prairie chickens or pheasants were found; low nest densities were found for bobwhites, dickcissels (*Spiza americana*), red-wings and cottontails; but relatively high densities of nests were found for meadowlarks. During the second or later nesting season following a prescribed burn, nest densities for prairie chickens, pheasants, mourning doves (*Zenaida macroura*), eastern meadowlarks (*Sturnella magna*), red-wings, dickcissels, field sparrows (*Spizella pusilla*), sedge wrens (*Cistothorus platensis*), and cottontails were all higher than were nest densities in prairie grass that had not been burned. Nest densities for small mammals were highest in unburned stands of prairie grass. Management recommendations are listed.

INTRODUCTION

Prairie and its modifiers, fire and grazing, have been absent for about a century from the ecology of grassland wildlife in Illinois. Prairie remnants of only about 3,440 ha (Graber and Graber 1976) remain from the estimated ⅔ or more of the state covered by prairie in 1810-20 (Anderson 1970). Despite the loss of prairie, prairie chickens (*Tympanuchus cupido*) and other grassland fauna have persisted locally at relatively high densities on "substitute prairies" in southeastern Illinois. The vegetation of these sites is chiefly introduced cool-season grasses managed for seed production, forage legumes, and weedy forbs (Yeatter 1943, 1963; Sanderson et al. 1973; Westemeier 1973, 1980; and Vance 1976). For this reason, redtop (*Agrostis alba*), timothy (*Phleum pratense*), brome (*Bromus inermis*), and legumes, such as red clover (*Trifolium pratense*) and Korean lespedeza (*Lespedeza stipulacea*), have been used to expedite the establishment of nest cover on sanctuaries acquired and managed to preserve 2 remnant flocks of prairie chickens in Illinois.

Sanctuary acquisition and management in Illinois have been cooperative efforts involving the Prairie Chicken Foundation of Illinois (disbanded since 1973), The Nature Conservancy, the Illinois Department of Conservation, the Illinois Natural History Survey, the Illinois Nature Preserves Commission, and several private conservationists. Up to 1982, 664 ha had been acquired. Efforts have focused on areas near Bogota, Jasper County (Fig. 1), and Kinmundy, Marion County. Recently, the Central Illinois Public Service Company designated an 81-ha tract at the Newton Power Station near Bogota for prairie chicken management. Most of the land in sanctuaries had been cropped for over a century prior to its acquisition. The former prairies in the sanctuary areas occurred as patches and strips between watercourses (Anderson 1970).

Although most native species of grassland wildlife readily accept and, in some instances, thrive on exotic vegetation, it has long seemed axiomatic that the reestablishment

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[1] Contribution from Illinois Federal Aid Project W-66-R (in part), the Illinois Department of Conservation, the U.S. Fish and Wildlife Service, and the Illinois Natural History Survey, cooperating. Direct inquiries to Westemeier, 618-783-4125.

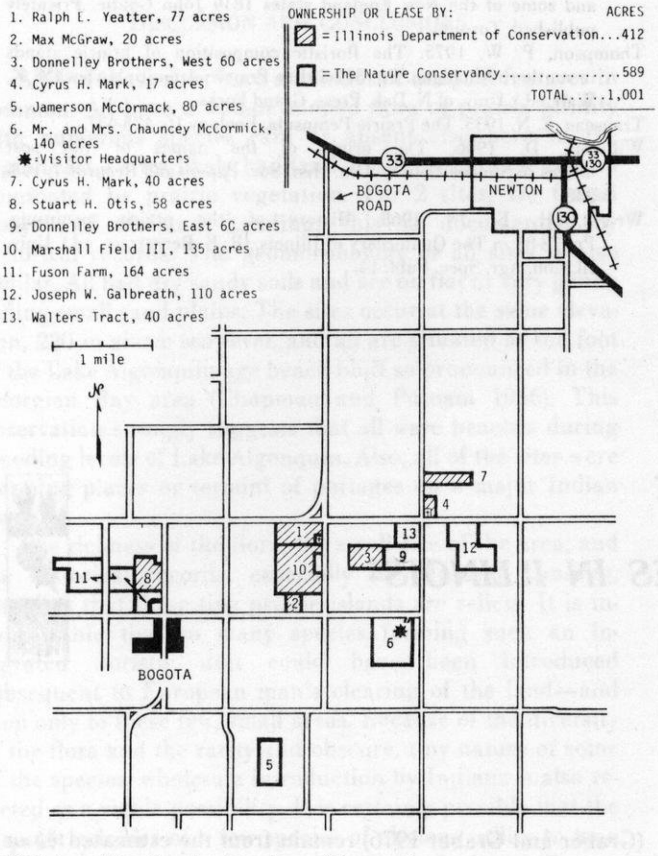

FIG. 1. Map Showing Locations of Sanctuaries.

and maintenance of native vegetation should be emphasized in management for prairie chickens and associated grassland wildlife (Yeatter 1963; Westemeier 1971, 1973). Thus, since 1963 selected fields on 6 of the 7 sanctuary units near Bogota have been seeded to prairie grasses. Cool-season introduced grasses and domestic legumes, however, have continued to provide about ¾ of the vegetation managed for nest cover on the sanctuaries.

The research described in this paper is part of a continuing long-term study initiated by the Illinois Natural History Survey near Bogota in 1963. The primary purposes of the nest study have been to develop data bases on the nesting ecology of prairie chickens from which to evaluate cover management programs as to acceptability, nesting success, and cost effectiveness and to provide a demographic basis for population analysis.

There have been few studies of the response of avian communities to the burning of prairie (Risser et al. 1981:424) or to grassland management of any kind (Skinner 1975). The purpose of this report is to summarize our data on responses of nesting grassland wildlife, with emphasis on prairie chickens, to seeded and naturally restored (in part) stands of managed prairie grasses. Management has included prescribed burning followed by high mowing, haying, and non-disturbance.

METHODS

The study area and the fairly standard techniques of prescribed burning have been described by Westemeier (1973). Nests were located by making systematic, intensive searches on foot from late May through late July. The nest-searching crew usually consisted of 2-4 persons walking side by side, each covering a 1.5-m swath and using a 1.5-m stick to part the cover in an attempt to view each possible nest site. Swaths to be searched were measured and straight lines were maintained by the use of steel marker poles topped with 3.8-l plastic jugs. Typically, each nest searcher could thoroughly search 1.4 ha per 8-hr day. Nests were identified by the shape, size, and color of eggs; the construction, shape, and size of nests; and sometimes by the presence of feathers, young, or adults. Each field was searched only once each summer, and some nesting could have occurred after a field had been searched. Also, some nests undoubtedly were missed. Primary emphasis was on locating prairie chicken nests.

TABLE 1. Area and fields of prairie grass searched for nests of birds and mammals, according to management practice prior to each nest season, on prairie chicken sanctuaries, Jasper County, Illinois, 1967-81.

Burn	Hectares (and no. of fields) searched			
Status	Undisturbed	Mowed	Hayed	Totals
Unburned	48.2 (28)	24.0 (14)	14.2 (8)	86.4 (50)
Burn I[a]				39.8 (18)
Burn II	13.5 (5)	17.4 (7)	17.5 (6)	48.4 (18)
Burn III	27.3 (9)	11.0 (4)	9.1 (4)	47.4 (17)
Burn IV	11.6 (7)	2.3 (3)	1.5 (2)	15.4 (12)
Burn > V	8.9 (6)	6.4 (7)	12.6 (11)	27.9 (24)
Totals	109.5 (55)	61.1 (35)	54.9 (31)	265.3 (139)

[a] Burn I = 1st nest season after burning.

Nest densities for each species have been expressed as nests or hatches per 4 ha, because 4 ha (10 acres) is the average size of fields on the prairie chicken sanctuaries. Nest success for the 3 galliforms was calculated as the percentage of nests of known fate that contained 1 or more hatched eggs. Detailed descriptions were made of all nest sites except those of red-winged blackbirds. Fields where hay had been cut just prior to a nest search were deducted from the density calculations for those species that nest off the ground, as such nests are often incorporated into hay bales and are unavailable for census. Evidence of nests of ground-nesting birds nests usually persists after haying.

Ideally, the data to be analyzed would have been derived from an experimental design based on replicated plots to assure that animals would have random access to various cover types and management practices. Unfortunately, replicated plot designs were impractical. We could only relate use by wildlife to those cover types available in any year. The long time series, 15 years, induced some semblance of randomness in the accessibility of different cover types to wildlife.

Although sample sizes of nests in total were relatively large, they quickly become limiting when categorized by management practices and time elapsed since burning. The analysis further suffered from differences in the abundance of potential nesters among years. We recognize that nest densities are not necessarily equatable with bird populations. Also, high nest densities do not necessarily imply habitat preference. Re-nesting following predation or nest success and unused nests by some species may increase nest density. However, patterns in nest numbers and success have emerged and warrant consideration. Chi-square tests (Steel and Torrie 1960) were used in analysis.

Over the years 1963-70, 24 fields containing mostly mixed Blackwell switchgrass (*Panicum virgatum*),[2] Nebraska 54 Indian grass (*Sorghastrum nutans*), and Kaw big bluestem (*Andropogon gerardii*) and ranging from 0.3 to 4.5 ha were established by seeding at the rate of about 2.2 kg of each species per ha by hand broadcasting. Little bluestem (*Andropogon scoparius*) and Trailway side-oats grama (*Bouteloua curtipendula*) at similar rates were included in some of the seedings. Except for some little bluestem, most of these 2 grasses never became established and disappeared within 3 years as the larger grasses became dominant. It is probable that the latter, more xeric grasses were at a disadvantage on much of the study area. Redtop and timothy at the rate of about 2.2 kg per ha each were added to the prairie grass seedings to expedite the development of nest cover, to control weeds, and to provide fuel for prescribed burning.

The 16.2-ha Walter's tract (Fig. 1), unplowed since the mid-1950's and acquired by The Nature Conservancy in 1973, was not seeded and has re-

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[2] Plant nomenclature follows Scott and Wasser (1980). Varieties indicated were those used by a commercial dealer in Nebraska.

TABLE 2. Nest densities for 3 galliform birds (including nest success) and the mourning dove in prairie grass fields according to burn and nonburn history prior to the nest season.

BURN CATEGORY OR NEST SEASON (I-V) SINCE FIRE	NESTS PER 4 HA (NO. OF NESTS)						
	PRAIRIE CHICKEN		PHEASANT		BOBWHITE		MOURNING DOVE
	TOTAL	HATCHED	TOTAL	HATCHED	TOTAL	HATCHED	
Unburned	0.5 (10)	0.2 (4)	0.1 (2)	0.05 (1)	0.9 (19)	0.6 (12)	0.1 (1)
Burn I	(0)	(0)	(0)	(0)	0.3 (3)	(0)	0.1 (1)
Burn II	1.0 (12)	0.4 (5)	0.5 (6)	0.1 (1)	0.9 (11)	0.5 (6)	0.7 (8)
Burn III	0.8 (9)	0.3 (4)	0.4 (5)	(0)[b]	0.2 (2)	0.1 (1)	0.3 (3)
Burn IV	1.3 (5)	(0)	0.5 (2)	(0)[b]	(0)	(0)	1.1 (4)
Burn ≥ V	2.3 (16)	1.3 (9)	0.6 (4)	0.3 (2)	(0)	(0)	0.1 (1)
Totals	0.8 (52)[a]	0.3 (22)	0.3 (19)	(4)	0.5 (35)[a]	0.3 (19)	0.3 (18)[a]

[a] $P < 0.01$.

[b] Two clutches were collected from each of these categories prior to possible hatching.

mained largely undisturbed except for prescribed burning conducted in late winter of 1974, 1976, 1979, and 1982. The burns have apparently facilitated the slow natural spread of prairie plants from roadsides, fencerows, and a wooded waterway. Today the Walter's tract comprises 75% native prairie vegetation and 25% woodland. The prairie vegetation presently consists predominantly of little bluestem, but patches of big bluestem, Indian grass, broom sedge (*Andropogon virginicus*), and prairie forbs are also conspicuous.

Management of plots seeded to prairie grasses has ranged from no disturbance (undisturbed) for several consecutive years to annual haying in midsummer, plus burning in late winter at 3- to 5-year intervals. Most haying, however, was done in mid-July in alternate years or every third year. Fields classified as high-mowed were either rotary mowed in late summer (for weed control or nesting enhancement) or harvested for seed (with a combine), resulting in stubble heights of 30 to 50 cm. Grazing of prairie grasses has not been employed to date, owing to inadequate fencing, lack of water, and a reluctance of local farmers to graze a forage with which they have had no prior experience.

RESULTS

A total of 139 fields (265 ha) dominated by prairie grasses was searched for nests of ground-nesting birds and mammals on prairie chicken sanctuaries on the Bogota Study Area over the 15 years, 1967 to 1981 (Table 1). Avian nests found by searching totaled 964, including red-winged blackbird (*Agelaius phoeniceus*), 693; dickcissel (*Spiza americana*), 91; prairie chicken, 52; northern bobwhite (*Colinus virginianus*), 35; eastern meadowlark (*Sturnella magna*), 27; ring-necked pheasant (*Phasianus colchicus*), 19; mourning dove (*Zenaida macroura*), 18; field sparrow (*Spizella pusilla*), 15; sedge wren (*Cistothorus platensis*), 9; American woodcock (*Scolopax minor*), 3; and 1 each for grasshopper sparrow (*Ammodramus savannarum*) and mallard (*Anas platyrhynchos*). One upland sandpiper (*Bartramia longicauda*) nest was found in an unsearched field. Cottontail (*Sylvilagus floridanus*) nests totaled 44, and small mammal (*Microtus ochrogaster* and *Synaptomys cooperi*) nests totaled 2,656 in the searched fields.

Switchgrass was the most frequently occurring prairie grass at nests of prairie chickens, pheasants, quail, meadowlarks, red-wings, dickcissels, and sedge wrens. Indian grass and big bluestem occurred at nests made by prairie chickens and 7 other species of birds. Little bluestem, which was mostly limited to the Walter's tract, occurred most frequently at nests made by field sparrows and woodcocks; some of the nests by pheasants, quail, and red-wings included little bluestem.

Nest Densities

Galliforms and doves. Nests of prairie chickens, quail, and doves were not randomly ($P < 0.01$) distributed among the available unburned and post-burn stands of prairie grass (Table 2). Curiously, the highest densities of prairie chicken nests in prairie grasses occurred in the 5th or later spring following burning. Among unburned and post-burn fields, collectively, prairie chickens showed a preference ($P < 0.01$) for those that were high-mowed (Table 3). No particular preferences for post-burns (Table 2) or management type were suggested for pheasants for the small sample of 19 nests; nor, did quail or doves, 32 and 17 nests, respectively, show a significant preference for management type (Table 3). Recently burned prairie grass was generally

TABLE 3. Nest data for 3 galliform birds and the mourning dove in fields of prairie grass according to management prior to the nest season.

PRAIRIE GRASS MANAGEMENT	NESTS PER 4 HA (NO. OF NESTS)						
	PRAIRIE CHICKEN		PHEASANT		BOBWHITE		MOURNING DOVE
	TOTAL	HATCHED	TOTAL	HATCHED	TOTAL	HATCHED	
Undisturbed	0.7 (19)	0.3 (8)	0.4 (10)	(1)[b]	0.8 (21)	0.4 (11)	0.3 (8)
High mowed	1.6 (24)	0.7 (11)	0.3 (5)	0.1 (2)	0.5 (8)	0.4 (6)	0.5 (7)
Hayed	0.7 (9)	0.2 (3)	0.3 (4)	0.1 (1)	0.2 (3)	0.1 (2)	0.1 (2)
Totals	0.9 (52)[a]	0.4 (22)	0.3 (19)	(4)[b]	0.6 (32)	0.3 (19)	0.3 (17)

[a] $P < 0.01$.

[b] Four clutches were collected from this category prior to possible hatching.

TABLE 4. Nest densities for 5 passerine birds in prairie grass fields according to burn or nonburn history prior to the nest season.

BURN CATEGORY OR NEST SEASON (I-V) SINCE FIRE	NESTS PER 4 HA (NO. OF NESTS)				
	EASTERN MEADOWLARK	RED-WINGED BLACKBIRD	DICKCISSEL	FIELD SPARROW	SEDGE WREN
Unburned	0.3 (6)	7.0 (104)	1.8 (27)	0.2 (3)	0.1 (1)
Burn I	0.5 (5)	7.5 (64)	0.6 (5)	(0)	0.1 (1)
Burn II	0.5 (6)	20.3 (208)	1.9 (19)	0.1 (1)	(0)
Burn III	0.3 (3)	18.9 (196)	2.4 (26)	0.8 (9)	0.6 (6)
Burn IV	0.3 (1)	25.5 (89)	0.6 (2)	0.6 (2)	0.3 (1)
Burn ≥ V	0.9 (6)	4.7 (32)	1.8 (12)	(0)	(0)
Totals	0.4 (27)	12.6 (693)^b	1.7 (91)^a	0.3 (15)^b	0.2 (9)^a

$^a P < 0.05$.
$^b P < 0.001$.

avoided; only 3 quail nests (none hatched) and 1 dove nest were found there (Table 2).

Passerines and other birds. Red-winged blackbird nests constituted 72% of the sample of 964 bird nests found in prairie grasses. Chi-square tests showed highly significant ($P < 0.001$) differences between observed and expected nest densities for red-wings in nest seasons following burning and other management. Red-wings selected for post-burns II, III, and IV (Table 4) and for high mowing (Table 5). Dickcissels, the second-most abundant nesting bird, showed a peak density of 2.4 nests per 4 ha in the third nest season following a burn and a preference ($P < 0.001$) for stands of prairie grass that had been hayed. Peak densities of nests of field sparrows and sedge wrens also occurred in the burn III category. Like dickcissels, sedge wrens also showed highest use of hayed stands, but field sparrows appeared partial to undisturbed stands. Nesting eastern meadowlarks were apparently nonselective relative to burned and unburned types and to mowing status of prairie grass.

The 3 woodcock nests found during this study were located in an undisturbed stand of little bluestem in the third nesting season following a winter burn. The woodcock nests were within 18 m of the wooded draw on the Walter's tract. One upland sandpiper nest was found in a prairie grass field that had recently been burned.

Mammals. Nest densities for cottontails and small mammals (Tables 6 and 7) showed significant departures from random expectations relative to burn type ($P < 0.01$) and other management ($P < 0.01$). Cottontails apparently preferred third-year post-burns that were undisturbed, whereas the small mammals showed a preference for the prairie grass plots that were both unburned and undisturbed. Curiously, nest densities for small mammals in the older post-burns did not return to the density levels found in unburned prairie grass.

Nesting Success of Gallinaceous Species in Prairie Grass

Data on nest success by prairie chickens, pheasants, and quail are included in Tables 2 and 3; however, owing to small sample sizes of hatched nests, it was not possible to determine significant ($P > 0.05$) differences in nest success relative to burning or other management practices conducted prior to nesting seasons. The highest densities of hatched prairie chicken nests were associated with the fifth or later spring following burning and with high mowing. Highest densities of hatched quail nests were found in unburned plots and in plots 2 springs after burning that were either undisturbed or high-mowed in the year prior to nesting.

Nest success by prairie chickens, pheasants, and quail was also considered in relation to the degree of nest concealment provided by prairie grasses (Table 8). These data were mostly for nests in fields dominated by prairie grass, but the data also included nests from fields not dominated by prairie grass but which had prairie grass at the nest sites. For 90 prairie chicken nests, success decreased significantly ($P < 0.05$) as the quantity of the prairie grasses concealing the nests increased; success ranged from 68.8% with vegetation other than prairie grass to only 14.3% when nests were fully concealed by prairie grasses. Bobwhite nests may have also been more successful (85.7%) when prairie grasses were

TABLE 5. Nest densities for 5 passerine birds in fields of prairie grass according to management prior to the nest season.

PRAIRIE GRASS MANAGEMENT	NESTS 4 HA (NO. OF NESTS)				
	EASTERN MEADOWLARK	RED-WINGED BLACKBIRD	DICKCISSEL	FIELD SPARROW	SEDGE WREN
Undisturbed	0.3 (7)	7.5 (206)	1.0 (27)	0.4 (12)	0.1 (3)
High mowed	0.4 (6)	19.4 (297)	1.6 (24)	0.2 (3)	(0)
Hayed	0.7 (9)	9.2 (126)	2.6 (35)	(0)	0.4 (5)
Totals	0.4 (22)	11.2 (629)^b	1.5 (86)^b	0.3 (15)^a	0.2 (8)^a

$^a P < 0.05$.
$^b P < 0.001$.

TABLE 6. Nest densities for cottontails and for prairie voles and southern bog lemmings (combined) in fields of prairie grass according to burn history prior to the nest season.

	NESTS PER 4 HA (NO. OF NESTS)	
BURN CATEGORY	COTTONTAILS	SMALL MAMMALS
Unburned	0.8 (18)	58.3 (1,246)
Burn I	0.1 (1)	21.7 (213)
Burn II	0.1 (1)	37.5 (449)
Burn III	1.7 (20)	42.0 (492)
Burn IV	1.1 (4)	32.0 (122)
Burn $\geq$ V	(0)	19.4 (134)
Totals	0.7 (44)[a]	40.5 (2,656)[a]

[a] P . 0.01.

absent, but success of pheasant nests increased (nonsignificantly) with increased prairie grass concealment. In comparison with our findings, Klimstra and Roseberry (1975) reported an average success rate of 33.7% for 863 bobwhite nests subjected to a variety of field conditions in southern Illinois.

Observations During Prescribed Burning

An average of 1.1 pheasants and 1.2 cottontails per ha were flushed during burning of 15 fields totaling 66.8 ha of prairie grass during the winters of 1979 through 1981 at Bogota. These data were based on minimum counts. The only field from which no pheasants were flushed had been rotary mowed during the previous August; all other fields were rank, undisturbed stands of prairie grass. No prairie chickens were flushed from any of the 15 fields of burning prairie grasses. For whatever reason, the use of rank stands of native prairie grasses by prairie chickens as diurnal cover during winter was low. Casual observation suggests that the nocturnal use by prairie chickens is also low but that pheasants use such cover extensively for nocturnal roosting sites during winter.

DISCUSSION

The frequent occurrence of switchgrass at the nest sites of a majority of the nests observed in prairie grasses was probably related to the predominance of switchgrass in most seeded stands of prairie grasses. Occurrences of Indian grass, big bluestem, little bluestem, and broom sedge at nest sites appeared to be roughly in proportion to their availability in the fields studied.

Little bluestem was reported as an important grass for nesting prairie chickens by Jones (1963) in Oklahoma and by Drobney and Sparrowe (1977) in Missouri, although Svedarsky (1979) reported big bluestem as the most important plant at nest sites in native vegetation in Minnesota. The lack of little bluestem at any of the prairie chicken nests in this study was not surprising, even though we have long believed little bluestem to be desirable for nesting prairie chickens. Although it occurred sparsely in several of the seeded plots, little bluestem was abundant on the 16.2-ha Walter's tract within 0.4 km of a major booming ground (area used for display and mating) and readily available to nesting prairie chickens. However, we found no prairie chicken nests in any of the vegetational types constituted of the relatively diverse prairie flora of that tract.

Other factors may be involved. Pheasants, for example, nest, roost, and crow in substantial numbers on the Walter's tract. In Iowa, George et al. (1979) found high densities of pheasant nests in seeded stands of little bluestem and switchgrass. Vance and Westemeier (1979) described the competitive threat by pheasants to the survival of Illinois prairie chickens. Also, about 4.5 ha of heavily wooded waterway transected the Walter's tract, and prairie chickens seemingly do not nest close to tall woody vegetation. Mammalian and avian predators are common on the sanctuary. In Minnesota, Svedarsky (1979) found predation on prairie chicken nests to be associated with proximity to brushy cover. Thus, the combined influence of pheasants, woody cover, and predation may have been sufficient to inhibit use of the Walter's tract by prairie chickens.

The responses by nesting prairie chickens to prairie grasses after burning was generally similar to their response following the burning of cool-season grasses (Westemeier 1973, unpublished), except that nest densities in prairie grasses were generally lower than they were in cool-season grasses. However, densities and success of prairie chicken nests in post-burn stands of prairie grass that had been high-mowed, compare favorably with those of prairie chickens nesting in redtop and timothy.

The long history of prairie chicken use of meadows farmed for grass seed as "substitute prairies" in southeastern Illinois (Leopold 1931; Yeatter 1943, 1963;

TABLE 7. Nest densities for cottontails and for prairie voles and southern bog lemmings (combined) in fields of prairie grass according to management prior to the nest season.

	NESTS PER 4 HA (NO. OF NESTS)	
PRAIRIE GRASS MANAGEMENT	COTTONTAILS	SMALL MAMMALS
Undisturbed	1.3 (36)	51.1 (1,399)
High-mowed	0.2 (3)	42.1 (643)
Hayed	0.3 (4)	29.2 (401)
Totals	0.8 (43)[a]	43.3 (2,443)[a]

[a] P 0.001.

TABLE 8. Nest success by 3 galliform birds according to the quantity of prairie grass at the nest site. Data are from nests in fields dominated by prairie grasses and from other nest sites that contained some prairie grasses for concealment.

	NEST SUCCESS (NO. OF NESTS)		
DEGREE OF CONCEALMENT OF NESTS BY PRAIRIE GRASS	PRAIRIE CHICKEN[a]	RING-NECKED PHEASANT	BOBWHITE
None	68.8 (32)	33.3 (3)	85.7 (14)
Partial	41.0 (44)	36.4 (11)	38.9 (18)
Full	14.3 (14)	50.0 (4)	66.7 (6)
Totals	46.7 (90)	38.9 (18)	60.5 (38)

[a] Differences significant P . 0.05.

Westemeier 1973, 1980) and in Missouri (Schwartz 1945) suggests both preference for and survival value from the use of relatively uniform vegetation about 30 cm tall for nesting. The importance of continuous, as opposed to scattered and bunched, plant structure of acceptable height for greater prairie chickens was considered by Jones (1963), and the concept has been strengthened recently by Buhnerkempe et al. (unpublished). A significant proportion of the unsuccessful prairie chicken nests in Table 8 were concealed by clumps of switchgrass, big bluestem, or Indian grass. We suspect that predators use clumps of vegetation as visual cues in April and May in their search for avian prey—often the eggs and young of red-wings and dickcissels, which typically nest in such clumps, particularly during the second, third, and fourth springs following burning (Table 5). Nests of prairie chickens that are established in vegetative clumps in those post-burn years probably have a higher risk of predation (Table 8) both because (1) nests (mostly red-wing) are often there and so predators tend to search these sites and (2) predators are more common or spend more time in these fields where prey are most numerous. Lawrence (1966) reported an increase in the numbers of mammalian predators during the 2nd and 3rd years after a burn in chaparral vegetation that reduced shrubs and increased grass coverage.

Rotary mowing and harvesting (by combine) of prairie grass for seed impart a more uniform structure, which in some manner enhances nest densities and success for prairie chickens in the following spring (Table 3). Predators apparently have more difficulty finding prairie chicken nests in relatively uniform mowed stands than in undisturbed or hayed stands, or the mowed stands are not as attractive to predators, particularly by the fifth or later nest season after burning, when red-wing nesting is minimal. Interspecific relationships can apparently play a role in nest placement by and success of prairie chickens. Dunn (1977) found the nests of tits (*Parus* spp.) had lower probabilities of predation when not located near nests of other species.

Hamerstrom et al. (1957:12) alluded to the importance of structure (height and density) rather than species composition of grasslands for prairie chickens in Wisconsin. Hamerstrom and Hamerstrom (1963:883) also emphasized that prairie and prairie chickens are not inseparable, i.e., management could be successful without being dependent on native prairie grasses. In Minnesota, Svedarsky (1979) found higher use of planted brome (relative to availability) by nesting prairie chickens than of the native grasses that predominated on his study area. Thus, one must wonder about the distribution, vegetation selected, and cover structure used by nesting prairie chickens and other grassland wildlife on pristine eastern tallgrass prairies.

Sampson (1921:545) described the original prairies of glaciated southern Illinois based on statements from early settlers and careful study of relict prairies:

> The low prairie was dominated mainly by *Spartina Michauxiana*, *Calamagrostis canadensis*, and *Panicum virgatum*, while the more extensive prairie was dominated by *Andropogon furcatus*. Coarse herbs grew only as scattered individuals among the grasses. On the exposed clay *Andropogon scoparius* was abundant, and associated with it were many coarse herbs. A mixed association consisting of the two Andropogons, *Sorghastrum nutans*, and *Sporobolus heterolepis* may have occurred in transition zones on some of these clay areas.

Sampson's emphasis on big bluestem as the dominant on both the Illinoisan and Wisconsin drift gives the impression that the mesic prairies were essentially stands of big bluestem of low diversity. Relative to structure and species diversity, our seeded stands of prairie grasses may in fact resemble the original mesic prairie. Perceptions of the original Illinois prairie as a diverse profusion of several hundred species of grasses and forbs are probably mistaken. Even more significant is that, over winter, big bluestem weathers down into a flattened and lodged jumble of coarse canes. Also, by April, when prairie chickens and other prairie birds initiate their nests, the original prairie was typically flooded (Williams 1981). Such a habitat is diametrically opposed to our current concept of preferred nest habitat for prairie chickens. On the basis of nearly 900 nests, we perceive a relatively uniform, vertically-oriented stubble about 30 cm tall on adequately drained sites as quality nest habitat for prairie chickens.

It is possible that fires of the magnitude, frequency, and timing (mostly autumn) described by Williams (1981) and grazing by large herbivores (Edwards 1978) created a dynamic and diverse mosaic of vegetational conditions suitable for a variety of nesting wildlife on pristine prairie. Such a patchwork would be further enhanced by the rolling topography typical of good prairie chicken range. An opposing argument is that large expanses of pristine eastern mesic prairie were not quality nesting substrate for prairie chickens and other birds because of the combination of poor drainage, poor vegetational structure, and, perhaps at times, too frequent fires and excessive grazing. The ready acceptance by prairie chickens of monotypic stands of redtop, timothy, brome, and, in Wisconsin, even Kentucky bluegrass (*Poa pratensis*) (Hamerstrom et al. 1957; Westemeier 1971)—and our high-mowed prairie grass—may thus represent a substitute for a more xeric element of the former mesic eastern prairies, perhaps structurally similar to the hill prairies (Evers 1955) and sand prairies of Illinois.

In presettlement times prairie birds must have been closely attuned to fire and grazing. According to Risser et al. (1981:417) the effects of periodic fire on grassland generally are an increase in above-ground biomass production for the following 2 or 3 years, at least in areas with adequate water. On Trelease Prairie in central Illinois, after 2 to 3 years of fire exclusion, biomass production returned to levels characteristic of unburned stands (Hadley and Kieckhefer 1963). Numbers of grasshoppers and biomass also increase following burning of true prairie (Risser et al. 1981:424). On the Texas coastal prairie, Chamrad and Dodd (1973) noted after-fire changes of increases in prairie chicken (*T. c. attwateri*) foods (vegetation, seeds, and insects) and vegetational density and a reduction in vegetational mulch and height. Subsequent work by Kessler and Dodd (1978) with burning of Texas coastal prairie was similar, but results were more definitive. Prairie birds evidently respond to changes in biomass and insect abundance and probably to the increased vertical aspect of cover structure following fire, as illustrated by Kirsch and Kruse (1973).

Our undisturbed, unburned prairie grass plots developed the heavy mulch condition described by Weaver and Rowland (1952) and were attractive mainly to small mammals (Table 6 and 7). Small mammals have been found to be positively associated with litter depth (Tester and Marshall 1961). The decline in nest densities for small mammals following fire in our study is also in general agreement with findings by Moreth and Schramm (1973) who, working on restored prairie in Illinois, found that fire temporarily reduced the density of small mammal populations. Many animals show quick, positive responses to fresh burns or even to still-burning habitats for feeding and courtship (Stoddard 1963; Lawrence 1966; Edwards and Ellis 1969; Komarek 1969; Kessler and Dodd 1978). Lawrence (1966) noted an overall increase in nesting grassland birds in the 3 post-burn years, followed by a decline. Best (1979) noted an increase in the usage of preferred shrub-grassland but reduced usage of adjacent prairie grasses by field sparrows during a nest season following a late April burn in Illinois. In our study, nesting in the year after burning was largely restricted to quail (Table 2), meadowlarks, red-wings, dickcissels (Table 4), and small mammals (Table 6). We found 1 nest each of mourning dove, sedge wren, upland sandpiper, and cottontail in recent burns. In mesquite (*Prosopis* spp.) rangeland of Texas, Soutiere and Bolen (1973) found mourning doves nesting on the ground in high densities during the current year's burn, with densities decreasing in each of 2 succeeding years. In the Texas study, and in a study in Oklahoma (Downing 1959), densities of ground-nesting doves appear similar to those listed in Tables 2 and 3 for doves.

Two species, the pheasant and the meadowlark, were indifferent to burn category and other management practices (Tables 2, 3, 4, and 5). Although our nest densities for pheasants were much lower than those found by George et al. (1979) in seeded prairie grass, our overall density of 17.1 nests per 4 ha for all birds in all management classes of prairie grass was higher than that of the Iowa study. Skinner (1975) reported 29.6 nests per 4 ha for 7 grassland bird species in grazed grassland in his Missouri study, which included mostly introduced grasses and some native grasses. Our overall nest densities of 0.4 nest per 4 ha for meadowlarks (Tables 4 and 5) in prairie grass stands are much lower than those found by Roseberry and Klimstra (1970): 1.1 per 4 ha overall for 307 nests, but up to 10 per 4 ha in ungrazed pastures in southern Illinois.

Dickcissels and sedge wrens were the only species seemingly to show preference for hayed prairie grass (Table 5), i.e., to the regrowth (primarily switchgrass) following haying in the summer prior to nesting. Our nest densities for dickcissels in hayed prairie grasses appear similar to the densities thought by Fretwell (1973) to be critical for successful nesting by dickcissels. Surprisingly, neither Kendeigh (1941) nor Birkenholz (1973) reported dickcissels on the prairies they studied.

In conclusion, we suspect that the big bluestem prairies of the past had a poor height-density profile, were too poorly drained, and, perhaps in some years at least, were too frequently burned or too heavily grazed to serve as quality nest cover for prairie chickens and several other grassland nesters in spring. We believe that nesting prairie chickens were probably limited in their distribution to the drier, better-drained ridges and bluff prairies, which showed structures more in keeping with our current concept of preferred habitat. If even moderately mesic prairie stands were used by Illinois prairie chickens, they must have been dependent upon light to moderate grazing for maintenance of an acceptable structure for nesting (Drobney and Sparrowe 1977). Among the management approaches we have tried with prairie grasses, high mowing following fire is apparently a satisfactory approximation of preferred nest habitat on native prairies and substitute prairies for prairie chickens and most other prairie birds.

Native prairie rose (*Rosa carolina*) has been shown to be an important food for prairie chickens in Missouri (Toney 1980). Perhaps greater emphasis on the establishment of prairie forbs to enhance species diversity and the use of grazing (Skinner 1975; Kessler and Dodd 1978) is needed in our prairie restoration efforts. Improved nesting success and enhanced attractiveness to prairie chickens and other endemic grassland birds may result. Research is needed on these aspects of prairie habitat management.

MANAGEMENT RECOMMENDATIONS

When surface drainage is adequate, managed tall prairie grasses can provide suitable nest cover for prairie chickens, at least 7 other prairie birds, and cottontails. High mowing (above 30 cm) of prairie grasses is recommended in conjunction with prescribed burning at 3- to 5-year intervals (perhaps 1-3 years longer for prairie chickens, depending upon the degree of brush encroachment), particularly if grazing is not feasible. Annual burning is not recommended. Haying of prairie grass may be desirable, but probably at intervals of not more than once in 3 years. Limited grazing, however, is suggested as a more natural alternative to mowing due to the constraints imposed by energy conservation and economics. Leaving stands of prairie grass undisturbed for more than 1 year is not recommended. Because of the threat imposed by pheasants on the survival of remnant endangered flocks of prairie chickens in Illinois, burning of prairie grasses in the fall may be better than in spring because it reduces prime roosting cover for pheasants.

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SUCCESS IN A SECONDARY HABITAT: THE DICKCISSEL IN THE TALLGRASS PRAIRIE

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Abstract. The dickcissel (*Spiza americana*) is the most abundant species in the breeding-season community of the tallgrass prairie in the Flint Hills of Kansas. Yet prairie is not the most preferred habitat; nesting density is as much as 5 times greater in mature oldfield communities. As a result of low nest density, prairie dickcissels suffer a significantly higher frequency as well as intensity of parasitism by the brown-headed cowbird (*Molothrus ater*), which reduces the production of young because of the removal of host eggs by the female cowbird. Prairie populations with low nest density, on the other hand, have a decreased chance of nests being destroyed by predators. Thus there is an offsetting balance between the 2 major factors affecting nest success so that the daily survival rate and the production of young in a prairie nest are no different from a nest in the oldfield community.

INTRODUCTION

The diversity of birds in grassland communities during the breeding season is low (Cody 1966). Furthermore, there are few unique grassland bird species. In the tallgrass prairie of North America, only the greater prairie-chicken is limited to that community, while other bird species in the prairie occur in a variety of other habitats. The dickcissel is abundant on the prairie but is present in higher densities in oldfield communities (Zimmerman 1971). The purposes of this paper are to relate dickcissel population size to that of other species present during the breeding season on the Konza Prairie Research Natural Area, Riley and Geary Counties, Kansas, and to compare the effects of factors affecting dickcissel productivity in the prairie with those in the oldfield community.

STUDY AREA

Konza Prairie is a 3486-ha tract of bluestem (*Androgogon-Panicum-Sorghastrum*) prairie and associated gallery forest in the Flint Hills Upland of Kansas. The area is unglaciated and heavily dissected with steep-sided hills exposing limestone and shale layers. The ridges are typically flat with shallow, rocky soils, while the larger, wider valleys have deeper, more permeable soil.

Until its acquisition (in 2 parcels, 1971 and 1977) by The Nature Conservancy, Konza Prairie was a working cattle ranch maintained in good to excellent range conditions. Konza Prairie is now managed in an attempt to ascertain the pre-settlement ecosystem through a factorial experimental design that provides several intervals of burning (including unburned tracts) and different intensities of grazing. At the present time, however, neither native large herbivore (e.g., *Bison, Cervus, Antilocapra*) or domestic cattle grazing treatments have been implemented.

METHODS

During the breeding seasons of 1972-1974 and 1976-1978, bird populations were estimated by the spot-map method (Williams 1936) on an annually burned tract of 12.2 ha and on an unburned area of 28.8 ha. The data for 1979 are from Knodel (1980) and involved 2 annually burned and 2 unburned plots. In 1981 and 1982, population data were collected using a variable distance transect (Burnham et al. 1980) on 2 annually burned plots, 3 plots burned every 4 years, and 3 unburned areas. None of the areas studied has been grazed by cattle since 1971. For each year the data from all areas censused have been combined, and the relative frequency for each species computed by dividing the total individuals for each species across all plots by the total for all species.

In 1979, weekly nest densities of dickcissels were determined on the 12.2-ha burned plot and the 28.8-ha unburned plot. These values were added to dickcissel nest density data from 3 oldfields and used to relate the weekly incidence of brown-headed cowbird parasitism to the density of nests in the construction and egg-laying stages. Nests in the egg-laying, incubation, and brooding phases of the nesting cycle were used to calculate nest densities that were in turn correlated with predation rates determined by the exposure method (Mayfield 1961, 1975).

RESULTS AND DISCUSSION

Thirty-one species have been detected on censuses during the breeding season in ungrazed sites of the Konza Prairie Research Natural Area (Table 1). Only 12 of these species, however, have a mean relative frequency of over 1 percent, and just 4—dickcissel, brown-headed cowbird, eastern meadowlark and grasshopper sparrow—together contribute over two-thirds (68.2%) of the individuals present. The only tallgrass prairie sites studied by Cody (1968) and Wiens (1973) were grazed and they either ignored cowbirds or, because of the method used, could not evaluate the abundance of brown-headed cowbirds. Thus these data have little value for comparison with the data from Konza Prairie presented here except to support the generalization of low bird-species richness in grasslands. The presence of horned larks in the community studied by Cody is worth noting as it resulted from the inclusion of a heavily grazed area within his study plots (Zimmerman, personal observation). As Table 1 indicates, horned larks are not present on ungrazed tallgrass prairie sites.

In 7 of the 9 years the dickcissel was the most abundant species in the ungrazed grasslands of Konza Prairie and, on the average, was almost twice as abundant as any other species. Yet prairie is not the preferred habitat. The density of male dickcissels, frequency of polygyny (Zimmerman 1971), and mean weekly density of nests (Table 2) were higher in mature oldfield habitats than in the prairie. The higher densities in oldfields suggests greater suitability of this habitat (Fretwell and Lucas 1969). While this is true for the male, it is not true for the female (Zimmerman 1982). Both the production of young per nest (0.72 in oldfields,

TABLE 1. Relative frequency (%) of breeding season birds in the tallgrass prairie of Konza Prairie Research Natural Area, Kansas.

	YEAR									
SPECIES	1972	1973	1974	1976	1977	1978	1979	1981	1982	MEAN
Dickcissel	18	24	38	23	38	26	23	31	14	26.1
Brown-headed cowbird	20	17	11	17	16	17	7	13	15	14.7
Eastern meadowlark	18	10	11	17	11	14	13	15	18	14.1
Grasshopper sparrow	20	14	11	11	4	10	22	14	14	13.3
Red-winged blackbird	8	14	11	6	9	10	8	2	6	8.2
Mourning dove	5	7	4	9	4	7	6	5	7	6.0
Upland sandpiper	6	7	5	6	7	7	6	6	3	5.9
Henslow's sparrow	0	0	7	8	2	2	4	4	2	3.2
Common nighthawk	2	5	2	2	4	2	5	0.4	0.4	2.5
Northern bobwhite	2	2	0	2	2	2	0	0	2	1.3
Eastern kingbird	0	0	0	0	0	0	5	2	3	1.1
Common yellowthroat	0	0	0	0	2	2	1	1	3	1.0

Species present < 1% frequency: northern harrier, American kestrel, greater prairie-chicken, ring-necked pheasant, killdeer, yellow-billed cuckoo, great horned owl, red-headed woodpecker, northern flicker, northern rough-winged swallow, house wren, sedge wren, gray catbird, brown thrasher, Bell's vireo, common grackle, orchard oriole, northern oriole, American goldfinch (See Appendix for scientific names).

0.87 in prairie) and the daily survival rates of the nests (0.14 in oldfield, 0.14 in prairie) are the same in both habitats.

The equity between the 2 habitats for the female is a function of the difference in the primary causes for nest loss between the mature oldfields and the prairie. The 2 major factors affecting nesting success of dickcissels are loss of 1 to 2 eggs per nest due to host egg removal by the brown-headed cowbird (Zimmerman 1983) or predation, causing the loss of whole clutches. The low density of dickcissel nests on the prairie results in a high incidence of nest parasitism by cowbirds (Elliott 1978), since both the frequency (Spearman $R = -0.77$, $N = 26$, $P < 0.01$) and the intensity (Spearman $R = -0.84$, $N = 22$, $P < 0.01$) of nest parasitism are inversely related to nest density (Zimmerman 1983). Daily predation rates in the prairie, on the other hand, are low in comparison to those in oldfields (Zimmerman MS). For example, on any day during the 12-day incubation period, the chance of an oldfield nest being depredated is 6.4% while it is only 3.8% on the prairie ($F = 2.13$, df = 24,136, $P < 0.01$). If daily predation rates across the whole nesting period from egg-laying to fledging are compared between these 2 habitats, the probability for loss from predation is 104 times greater in oldfields than in prairies. This difference appears not to be a density-dependent association between nest density and daily predation rates, but rather a reflection of the higher density of predators in oldfield communities (Zimmerman MS).

TABLE 2. Weekly dickcissel nest densities (nests per ha) and other features of study sites.

	OLDFIELDS[1]			PRAIRIES	
FEATURE	1 YR. OLD	3 YR. OLD	5 + YR. OLD	UNBURNED	BURNED
Total area (ha)	22.7	22.7	30.4	28.8	12.2
Mean density	**0.22**	**0.78**	**0.64**	**0.15**	**0.23**
Standard error	0.050	0.191	0.115	0.023	0.052
Number	10	13	14	13	10

[1] Oldfield sites were located in Riley Co., KS on the Ft. Riley Military Reservation; see Zimmerman (1971) for vegetation structure.

While parasitism is high in the prairie, predation rates are low. In the oldfield, however, parasitism is low and predation rates are high. Thus when these 2 populations are compared, the 2 major factors affecting nest survival tend to offset one another so that daily nest survival probabilities are similar.

ACKNOWLEDGMENTS

We thank the Director, Konza Prairie Research Natural Area, Division of Biology, Kansas State University for his permission and cooperation in conducting this research. Partial support for this study was provided by a grant to Finck from the Chapman Memorial Fund of the American Museum of Natural History, New York, NY, while data from 1981 and 1982 were collected as part of the Long Term Ecological Research program at Konza Prairie funded by NSF grant DEB 8012166.

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APPENDIX 1. SCIENTIFIC NAMES OF BIRD SPECIES MENTIONED IN TEXT AND TABLES.

Northern harrier	*Circus cyaneus*
American kestrel	*Falco sparverius*
Ring-necked pheasant	*Phasianus colchicus*
Greater prairie-chicken	*Tympanuchus cupido*
Northern bobwhite	*Colinus virginianus*
Killdeer	*Charadrius vociferus*
Upland sandpiper	*Bartramia longicauda*
Mourning dove	*Zenaida macroura*
Yellow-billed cuckoo	*Coccyzus americanus*
Great horned owl	*Bubo virginianus*
Common nighthawk	*Chordeiles minor*
Red-headed woodpecker	*Melanerpes erythrocephalus*
Northern flicker	*Colaptes auratus*
Eastern kingbird	*Tyrannus tyrannus*
Horned lark	*Eremophila alpestris*
Northern rough-winged swallow	*Stelgidopteryx serripennis*
House wren	*Troglodytes aedon*
Sedge wren	*Cistothorus platensis*
Gray catbird	*Dumetella carolinensis*
Brown thrasher	*Toxostoma rufum*
Bell's vireo	*Vireo bellii*
Common yellowthroat	*Geothlypis trichas*
Dickcissel	*Spiza americana*
Grasshopper sparrow	*Ammodramus savannarum*
Henslow's sparrow	*Ammodramus henslowii*
Red-winged blackbird	*Agelaius phoeniceus*
Eastern meadowlark	*Sturnella magna*
Common grackle	*Quiscalus quiscula*
Brown-headed cowbird	*Molothrus ater*
Orchard oriole	*Icterus spurius*
Northern oriole	*Icterus galbula*
American goldfinch	*Carduelis tristis*

HABITAT SELECTION OF SMALL MAMMALS IN BURNED AND UNBURNED TALLGRASS PRAIRIE

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Abstract. During the spring and summer of 1981, live-trapping techniques were used to determine habitat selection of small mammals in a restored tallgrass prairie in western Illinois. Differences in small mammal composition of burned and unburned prairie were emphasized. Data were collected from 4 neighboring grids, 2 being located in freshly burned prairie and 2 in unburned prairie. Although 9 species of small mammals were captured, only 4—*Microtus ochrogaster* (prairie vole), *M. pennsylvanicus* (meadow vole), *Peromyscus maniculatus* (prairie deer mouse), and *P. leucopus* (white-footed mouse)—occurred in abundance. *M. ochrogaster* occurred in both burned and unburned prairie but was most abundant in the burned prairie. *M. pennsylvanicus* was caught primarily in unburned prairie. Both *P. maniculatus* and *P. leucopus* were caught almost exclusively in burned prairie. The habitat selection of these mammals is thought to be influenced primarily by the presence or absence of litter and secondarily by interspecific competition. Other species encountered were *Reithrodontomys megalotis* (western harvest mouse), *Zapus hudsonius* (meadow jumping mouse), *Blarina brevicauda* (short-tailed shrew), *Mus musculus* (house mouse), and *Sorex cinereus* (masked shrew).

INTRODUCTION

This paper reports part of a continuing, long-term study of small mammals in a restored tallgrass prairie in west-central Illinois. Studies on the effects of fire on animals, particularly birds and mammals, have been carried out over the past 17 years in the restored prairies at the Knox College Biological Field Station, 20 miles east of Galesburg, Illinois.

Fire has long been recognized as a natural element of grassland ecosystems. During periods of intermittent drought or dry, windy weather in autumn and spring, prairie was especially susceptible to fire (Jackson 1965). Lightning was a common natural cause of grass fires (Komarek 1964) and early man often started them to influence the presence, movements, and capture of large game animals (Risser et al. 1981). Before the continuity of the prairie was interrupted by white settlers, there were few barriers to the movement of fire once it started (Sauer 1950). Consequently, a single fire might spread over many square miles before dying out.

Many studies have shown that fire brings about abrupt changes in prairie habitat. Old (1969) and Hulbert (1969) demonstrated that fire may result in partial or complete removal of standing dead plant material and accumulated litter. Moreover, it may result in the complete removal of all vegetative cover which, in turn, causes changes in microclimatic conditions near the soil. Daubenmire (1968) recorded significantly greater diurnal temperature extremes near the soil after a fire than before. Although the immediate effects of fire are destructive, prairie vegetation is adapted to fire and in the long run is not harmed by it. Hadley and Kieckhefer (1963) found total plant biomass production and flowering in an Illinois prairie to increase after an early spring fire. The results of other studies suggest that these effects are due primarily to the removal of accumulated litter (Curtis and Partch 1950, Weaver and Rowland 1952, Hulbert 1969, and Old 1969). The recovery of prairie vegetation from an early spring fire may be complete by early summer (Hadley and Kieckhefer 1963), but the habitat afforded by the vegetation arising from a freshly burned prairie is markedly different from that of an unburned prairie. While the effects of fire on prairie vegetation are becoming increasingly well documented, its effects on the animal components of prairie are not well understood. This study attempted to document the habitat selection of small mammal species with regard to freshly burned prairie and unburned prairie with 2- and 3-year accumulations of litter and standing dead plant material. Specifically, this study examined species diversity, distribution, and abundance of small mammals in burned and unburned plots of restored prairie.

MATERIALS AND METHODS

Study Area

This study was conducted from 1 May to 31 August 1981 on 4 neighboring 0.16-ha plots of restored tallgrass prairie, hereafter referred to as grids (Fig. 1). The dominant vegetation of all the grids consisted of equal amounts of big bluestem (*Andropogon gerardii*) and Indian grass (*Sorghastrum nutans*). Switchgrass (*Panicum virgatum*) was well represented on Grid II as was the composite downy sunflower (*Helianthus mollis*). Other forbs present in significant amounts were white and yellow sweet clover (*Melilotus* spp.) particularly on Grid III. All grids had a very sparse scattering of other prairie forbs including *Petalostemum*, *Silphium*, *Helianthus*, *Lespedeza* and *Desmodium* species. Grids II and III were the burned plots; a fire conducted on 14 April 1981 consumed over 90% of the total vegetative cover on these grids. At no time during this study did these grids contain any significant amounts of litter or standing dead plant material. Grids I and IV were the unburned plots and had not been burned since spring 1978 and spring 1979 respectively. Both had a large amount of standing dead plant material and a dense accumulation of litter at ground level.

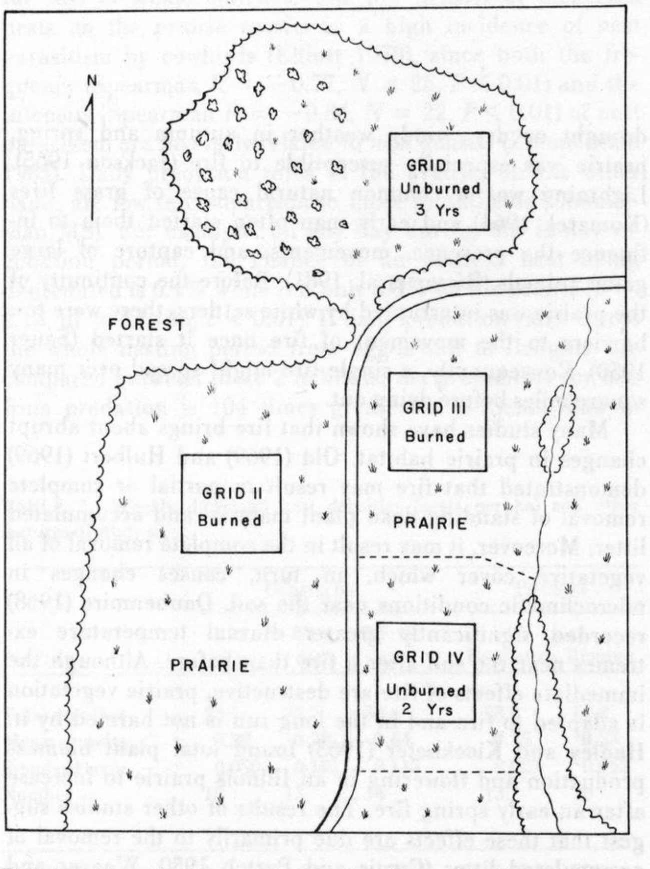


FIG. 1. Map of study area showing locations and habitats of burned and unburned trapping grids.

Trapping Methods

Each grid was a 40-m square with traps stationed at 8-m intervals and 36 traps per grid. One Sherman-type or Longworth-type live-trap was placed at each station, the 2 types being staggered throughout each grid. During each trapping night, all traps were baited with commercial bird seed in the late afternoon and checked the following morning. Between trapping nights, all traps were locked open and prebaited with seed. The total sample consisted of 47 nights of trapping completed during the 18 week period from 1 May to 31 August. All animals were toe-clipped upon first capture for identification purposes. No more than 1 toe was clipped per foot. The following information was recorded for each capture: grid, station, species, identification number, activity, weight, sex, condition of scrotum and testis (males) or of vagina, mammary glands, and pubic symphysis (females). Only species diversity, presence, and abundance data are presented in this paper.

Methods and Analysis

Relative abundance (total number of a given species in a particular grid) and frequency (total number of different stations in a particular grid at which a given species was caught) were calculated for all species, on each grid. From these, prominence values (relative abundance multiplied by the square root of the frequency) were calculated on a weekly basis (Kaufman and Fleharty 1974). Prominence value gives a more refined estimate of habitat use than density because it is sensitive not only to the total number of individuals of a species in a given area, but also the spatial activity of those individuals in that area. A modified version of the Simpson Diversity Index, given the name Reduced Simpson Diversity Index and hereafter referred to as RSD, was used to determine species diversity within each grid. To calculate a diversity index a measure of importance must be determined. The measure of importance must be a variable that accurately reflects the diversity of the community being examined. In this study prominence values were used as the measure of importance. The standard Simpson Diversity Index is calculated:

$$SD = 1 - \sum_{1}^{s} (n_i/N)^2$$

n = the measure of importance for each species (in this study, the prominence value for each species)

N = the total measure of importance (in this study, the sum of the prominence values for all species)

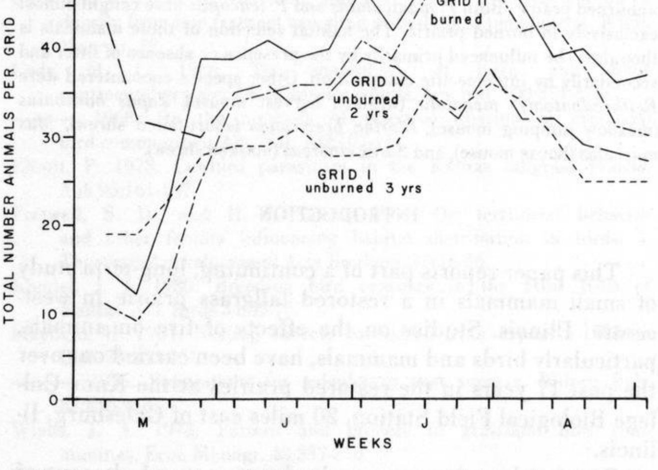


FIG. 2. Total number of animals present per grid throughout the trapping period.

TABLE 1. Total number of individuals and total number of captures (parentheses) for each mammal species on each grid.

SPECIES	GRID I (UNBURNED 3 YRS)	GRID II (BURNED)	GRID III (BURNED)	GRID IV (UNBURNED 2 YRS)
Microtus ochrogaster	24 (271)	66 (700)	68 (743)	52 (495)
Microtus pennsylvanicus	42 (579)	11 (40)	20 (91)	52 (396)
Peromyscus maniculatus	3 (4)	17 (139)	22 (313)	6 (28)
Peromyscus leucopus	1 (2)	24 (144)	7 (9)	0 (0)
Reithrodontomys megalotis	3 (15)	2 (14)	3 (6)	4 (19)
Zapus hudsonius	1 (1)	8 (11)	5 (6)	3 (3)
Blarina brevicauda	5 (18)	1 (1)	0 (0)	2 (2)
Mus musculus	1 (2)	0 (0)	1 (1)	2 (4)
Sorex cinereus	0 (0)	0 (0)	0 (0)	1 (1)

s = the number of species in the sample

SD = the Simpson Diversity Index

The RSD modification of the standard Simpson Diversity Index was calculated:

$$RSD = 1 - [\Sigma^{s} (n_i/N)^2 + SD/s]$$

The net effect of this modification is to make the standard Simpson Diversity Index more sensitive to the number of species in the sample. This modification was necessary because of the relatively small number of species encountered in this study. Abundance data were analyzed for weekly intervals. Population density was calculated using the minimum number known alive method. Hilborn et al. (1976) found that this method only slightly underestimates population density when "trappability" (number of individuals actually caught divided by the number known to be present, during a given period) is greater than 75%. Trappabilities for all species examined in this study remained above 80%. A boundary strip equal to the average distance between successive captures for a given species was added to a grid in order to determine the actual area sampled for that species. In the analysis of results, both Student's *t* and chi-square were used as tests of significance.

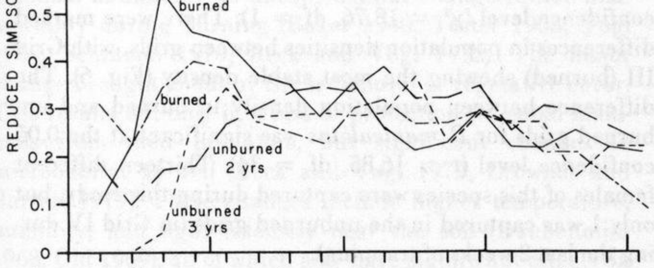


FIG. 3. Reduced Simpson Species Diversity Index (RSD) for each grid throughout the trapping period.

RESULTS

Total Abundance and Species Diversity

During this study 4058 captures were recorded for 457 individuals representing 9 species of small mammals (Table 1). In decreasing order of abundance these species were *Microtus ochrogaster, Microtus pennsylvanicus, Peromyscus maniculatus, Peromyscus leucopus, Reithrodontomys megalotis, Zapus hudsonius, Blarina brevicauda, Mus musculus* and *Sorex cinereus.* The 2 species of *Microtus* accounted for 73.3% of the total individuals and 81.6% of the total captures, while the 2 species of *Peromyscus* accounted for 17.5% of the total individuals and 15.7% of the total captures. The remaining 9.2% of the total individuals and 2.7% of the total captures was distributed among the other 5 species encountered.

With the exception of Grid IV, the total number of animals on each grid increased after the first week and peaked near the twelfth, during the month of July (Fig. 2). The total number of animals on all grids was decreasing at the time trapping was discontinued. The difference between total number of animals caught in burned and unburned grids for the trapping period as a whole was not significant

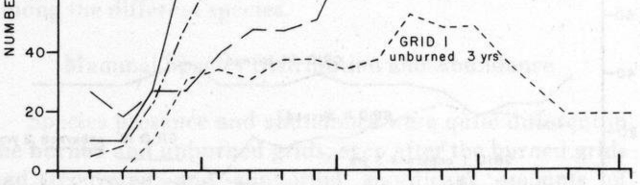


FIG. 4. Population density per hectare *Microtus ochrogaster* for each grid.

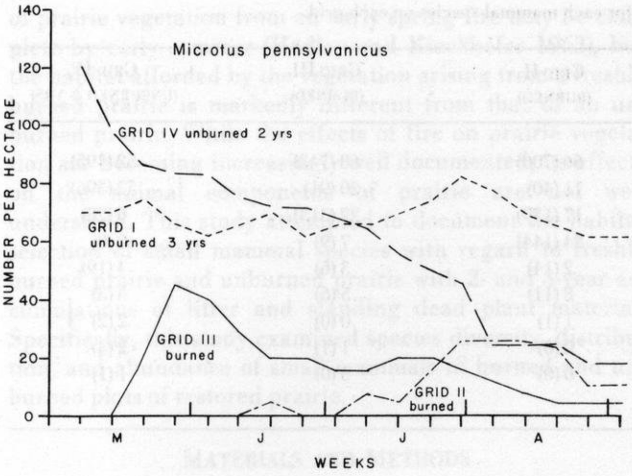


FIG. 5. Population density per hectare of *Microtus pennsylvanicus* for each grid.

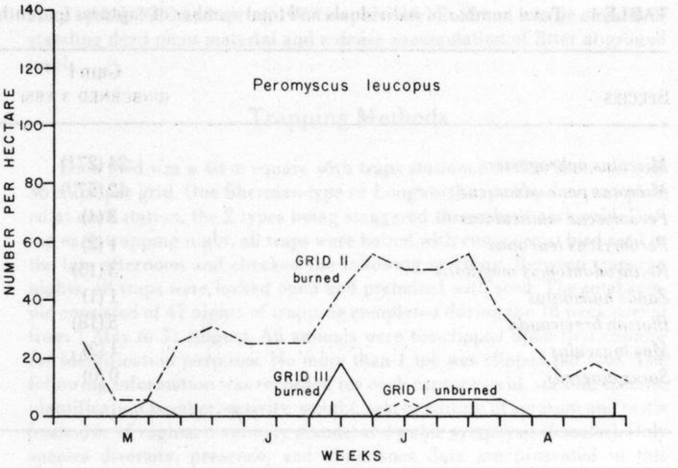


FIG. 7. Population density per hectare of *Peromyscus leucopus* for each grid.

at the 0.05 confidence level ($t = 1.75$, df = 34), but the difference between total number of animals caught in burned and unburned grids for both the first and second weeks of trapping was significant ($\chi^2 = 14.73$ for the first week and 12.50 for the second week, df = 1).

Species diversity in the burned and unburned grids seemed to peak during the third and eleventh weeks respectively (Fig. 3). The only major changes in species diversity occurred in Grids I and III during the month of May. There were no significant differences between the RSD values for burned and unburned grids ($t = 1.05$, df = 34).

Habitat Distribution of *Microtus* Species

Population densities of *M. ochrogaster* (prairie vole) and *M. pennsylvanicus* (meadow vole) suggest significant differences in their preferred habitats (Figs. 4, 5). After the third week of trapping *M. ochrogaster* was caught in abundance on all 4 grids but was considerably more abundant on the burned grids. The difference between the total number of individuals caught in burned and unburned grids (Table 1) for this species was significant at the 0.05 confidence level ($\chi^2 = 16.00$, df = 1). The July population high for this species in the burned grids was twice that of Grid IV (unburned 2 years) and about 3 times the level reached in Grid I (unburned 3 years). The difference between population densities in burned and unburned grids for *M. ochrogaster* was significant at the 0.05 confidence level ($t = 4.35$, df = 34).

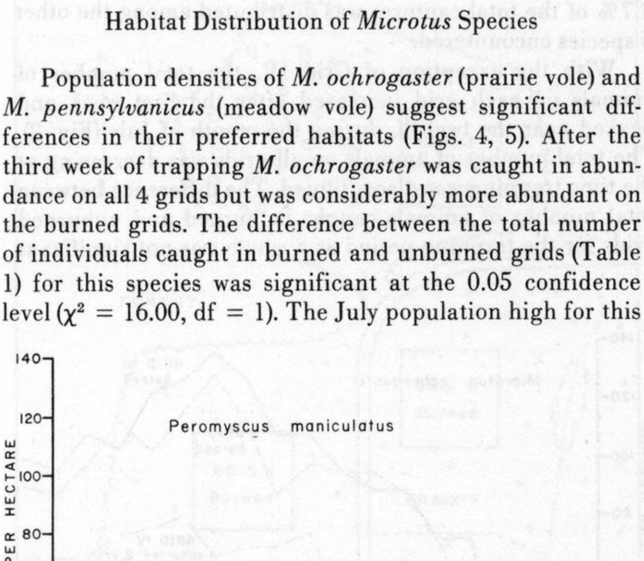


FIG. 6. Population density per hectare of *Peromyscus maniculatus* for each grid.

M. pennsylvanicus occurred primarily in the unburned grids. The difference between the total number of individuals in burned and unburned grids (Table 1) for this species was significant at the 0.05 confidence level ($\chi^2 = 31.76$, df = 1). There were marked differences in population densities of *M. pennsylvanicus* between grids. Grid I (unburned 3 years) showed a moderate and very stable density. Grid IV (unburned 2 years) showed a high initial population density that declined as the season progressed. With the exception of late May on Grid III, densities of M. *pennsylvanicus* remained low on the burned grids throughout the study. The difference between population densities in burned and unburned grids for this species was significant at the 0.05 confidence level ($t = 13.74$, df = 34).

Habitat Distribution of *Peromyscus* Species

Two species of *Peromyscus* were important components of the small mammal fauna in the study area. *P. maniculatus* (prairie deer mouse) was caught on all 4 grids but occurred primarily in the burned grids. The difference between total number of individuals in burned and unburned grids (Table 1) for this species was significant at the 0.05 confidence level ($\chi^2 = 18.76$, df = 1). There were marked differences in population densities between grids, with Grid III (burned) showing the most stable density (Fig. 6). The difference between population density in burned and unburned grids for *P. maniculatus* was significant at the 0.05 confidence level ($t = 16.85$, df = 34). Thirteen different females of this species were captured during this study, but only 1 was captured in the unburned grids (in Grid IV during the last 2 weeks of trapping).

P. leucopus (white-footed mouse) was caught in only 3 grids and occurred almost exclusively (save 2 captures) in the burned grids. The difference between total number of individuals in burned and unburned grids (Table 1) for this species was significant at the 0.05 confidence level ($\chi^2 = 28.12$, df = 1). Only Grid II (burned) maintained a continually active cohort of individuals (Fig. 7). The activity of these individuals was concentrated in the northwest corner of the grid (Fig. 9). The difference between population density in burned and unburned grids for *P. leucopus* was significant at the 0.05 confidence level ($t = 7.25$, df = 34).

Other Species Present

R. megalotis (western harvest mouse) was nearly evenly distributed among all 4 grids. The difference between total number of individuals in burned and unburned grids (Table 1) for this species was not significant at the 0.05 confidence level ($\chi^2 = 0.08$, df = 1). Five different females of this species were captured during this study, but on only 3 occasions were any 2 caught in the same grid. Throughout most of this study there was 1 female of *R. megalotis* per grid.

Z. hudsonius (meadow jumping mouse) occurred most frequently in the burned grids. The difference between total number of individuals in burned and unburned grids (Table 1) for this species approached significance at the 0.05 confidence level with $P < 0.054$ ($\chi^2 = 3.76$, df = 1). The difference between total captures in burned and unburned grids (Table 1) was significant at the 0.05 confidence level ($\chi^2 = 8.04$, df = 1).

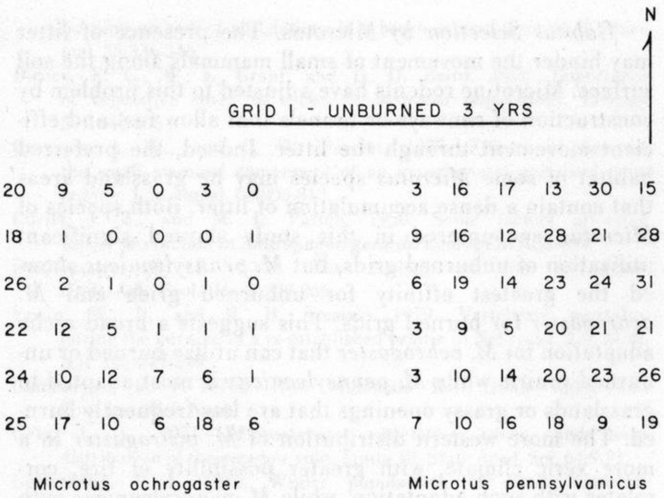
B. brevicauda (short-tailed shrew) occurred almost exclusively (save 1 capture) in the unburned grids (Table 1). The difference between total number of captures in burned and unburned grids (Table 1) for this species was significant at the 0.05 confidence level ($\chi^2 = 17.20$, df = 1). Not 1 individual of this species was caught until 15 July after 10 weeks of trapping.

Both *Mus musculus* (house mouse) and *Sorex cinereus* (masked shrew) were rare species during this study (Table 1).

DISCUSSION

Immediate Effects of Burning

Although the total abundance of small mammals was not significantly different in burned and unburned grids for the trapping period as a whole, there were significantly fewer animals in the burned areas during the first 2 weeks of trapping (Fig. 2). Erwin and Stasiak (1979) found very little evidence of small mammal mortality during the burning of a restored tallgrass prairie in Nebraska. In most studies of this kind, workers have attributed a reduction in small mammal abundance to abrupt habitat change rather than mortality during burning (Baker 1940, Tester 1965, Vogl 1967, Schramm 1970, Beck and Vogl 1972). The major change brought about by fire is removal of vegetative cover. This results not only in a loss of protection for small mammals from their predators, but significant changes in microhabitat as well (Beck and Vogl 1972, Crowner and Barrett 1979). These changes include higher temperature, humidity, and light intensity near the soil (Daubenmire 1968, Old 1969), all of which may have significant effects on small mammal activity (Getz 1971). While Getz (1971), Batzli (1974), and Birney et al. (1976) found a strong positive relationship between abundance of *Microtus* and amount of vegetative cover, Tester and Marshall (1961), Tester (1965), and Beck and Vogl (1972) reported *Peromyscus* in burned areas deficient in vegetative cover. The results of this study are in agreement. Only 5 individuals of *Microtus* were caught on the burned grids during the first 2 weeks of trapping as opposed to 23 individuals of *Peromyscus.* The initial difference in abundance between burned and unburned grids is the result of the extremely low number of *Microtus* in the burned grids during the spring. That, in turn, is viewed as a result of the nearly complete removal of vegetative cover from the burned grids.



20	9	5	0	3	0	3	16	17	13	30	15
18	1	0	0	0	1	9	16	12	28	21	28
26	2	1	0	1	0	6	19	14	23	24	31
22	12	5	1	1	1	3	9	5	20	21	21
24	10	12	7	6	1	3	10	14	20	23	26
25	17	10	6	18	6	7	10	16	18	9	19

FIG. 8. Spatial location of total captures for *Microtus ochrogaster* and *M. pennsylvanicus* on Grid II.

The rate of small mammal repopulation for a burned grassland area probably depends largely on the growth rate of the vegetation within that area, which varies between different plant communities. In this study, small mammal abundance in burned grids had surpassed that of unburned grids by the first of June, only 6 weeks after the time of burning. Such rapid rates of recovery are a reflection of the rapid growth of this prairie vegetation after it was burned and have not been reported previously for small mammals in such habitat.

Species Diversity

Species diversity was similar for burned and unburned prairie. Although species diversity in each grid remained rather constant throughout most of the trapping period, there were moderate fluctuations during the early weeks (Fig. 3). These might have been caused by spring burning but might also reflect differences in reproductive activity among the different species.

Mammal Species Distribution and Abundance

Species presence and abundance were quite different in the burned and unburned grids, even after the burned grids had recovered and supported significant amounts of vegetative cover. It is believed that there are 2 major factors responsible for these differences: habitat differences resulting from fire removal of litter and standing dead plant material, and interspecific competition.

Habitat Selection by Microtus. The presence of litter may hinder the movement of small mammals along the soil surface. Microtine rodents have adjusted to this problem by construction of runways or tunnels that allow fast and efficient movement through the litter. Indeed, the preferred habitat of some *Microtus* species may be grassland areas that contain a dense accumulation of litter. Both species of *Microtus* encountered in this study showed significant utilization of unburned grids, but *M. pennsylvanicus* showed the greatest affinity for unburned grids and *M. ochrogaster* for burned grids. This suggests a broad niche adaptation for *M. ochrogaster* that can utilize burned or unburned prairie while *M. pennsylvanicus* is most adapted to grasslands or grassy openings that are less frequently burned. The more western distribution of *M. ochrogaster* in a more xeric climate, with greater possibility of fire, correlates with such adaptation, while *M. pennsylvanicus* with its eastern and more northern distribution would encounter fire and absence of litter much less frequently.

The presence or absence of litter also influences the microclimate of *Microtus* habitat. According to Gottschang (1965) and Miller (1969) *M. ochrogaster* prefers dry or upland habitat, while *M. pennsylvanicus* prefers wet or lowland habitat. The work of Anderson (1965) and Old (1969) has shown that burned prairie has lower soil moisture than unburned prairie. The burned grids in this study may have offered drier habitat and a different microclimate than the unburned grids.

Risser et al. (1981) describes *M. ochrogaster* as a grassland species and *M. pennsylvanicus* as an ecotonal species inhabiting prairie-forest transition communities. The varied habitats available in this study provided suitable habitat for both species and their distribution and abundance on the different grids may well reflect the different centers of climate and habitat in which these species originally evolved.

The differences between Grid I (unburned 3 years) and Grid IV (unburned 2 years) may reveal the subtle way in which amount of litter may influence *Microtus* presence and abundance. In Grid I *M. pennsylvanicus* density appeared rather stable while *M. ochrogaster* density showed a moderate increase followed by a late summer decline. However, in Grid IV *M. pennsylvanicus* density gradually declined while *M. ochrogaster* density increased, becoming well established in the late summer. These observations may also reflect interspecific competition discussed below.

Competitive Exclusion Between Microtus *Species*. Interspecific competition may influence both the presence and habitat distribution of *Microtus* species where they occur sympatrically in tallgrass prairie. The brief "invasion" of Grid III (burned) by *M. pennsylvanicus* (Fig. 5) in late May (presumably from the adjacent unburned Grid IV) appeared to have been suppressed by the dramatic increase in *M. ochrogaster* density, which reached twice that of *M. pennsylvanicus* by early June. In Grid IV (unburned 2 years) a gradual decline in *M. pennsylvanicus* density coincided with a partially successful "invasion" by *M. ochrogaster*, which attained about half the density it attained in burned grids. The decline in *M. pennsylvanicus* density on this unburned grid was due partly to dispersal into the large burned area surrounding Grid IV, but might also have been influenced by competition from individuals of *M. ochrogaster* emigrating from the adjacent burned area.

In Grid I (unburned 3 years) *M. pennsylvanicus* density was most stable and *M. ochrogaster* density was lowest. Spatial occurrence of these species in Grid I was examined by plotting the total number of captures for each species at each trap station (Fig. 8). The occurrence of *M. ochrogaster* was limited almost entirely to the southwest corner of the grid suggesting that individuals "invaded" Grid I from the neighboring burned grids to the south and west after *M. pennsylvanicus* had reached a stable density. Since the physical and vegetational character of Grid I was uniform throughout, it appears that *M. pennsylvanicus* was able to exclude *M. ochrogaster* from an area with heavy accumulation of litter and standing dead plant material. Thus the presence or absence of fire over various lengths of time, coupled with interspecific competition, may be the determining factors in habitat distribution and niche separation of *Microtus* species sympatric in true prairie habitat.

Peromyscus *Distribution and Abundance*. Other species of rodents that utilize grasslands may not be as well adapted to accumulated litter as microtines. *P. maniculatus* and *P. leucopus* were caught almost exclusively in burned grids, where litter was absent. The pattern of locomotion in *Peromyscus* has been described as primitive ricochetal, involving a combination of short leaps and quick changes in direction (Gambaryan 1974). There is no evidence to indicate that these rodents construct runways through litter as do species of *Microtus*. The presence of litter may hinder their travel, increasing both their vulnerability to predators and energy expenditure during periods of above-ground activity. Unfavorable effects of litter seem to be the most plausible explanation for the absence of *P. maniculatus* and *P. leucopus* from the unburned grids. The activity of *P. leucopus* during this study supports this idea particularly well. This species is widely recognized as a woodland inhabitant and was probably not a resident on any of the trap-

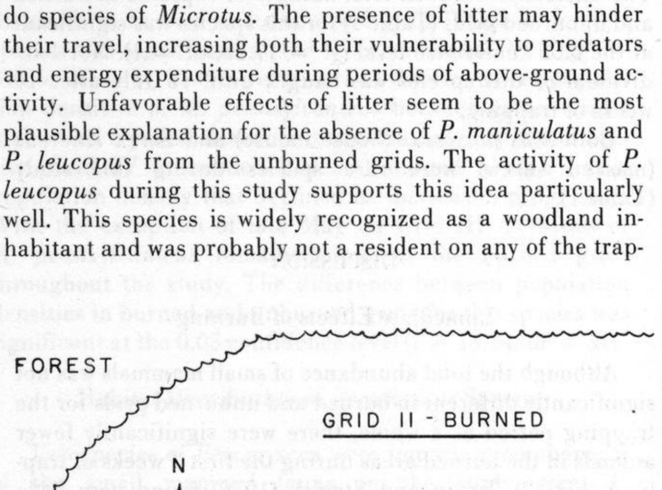


FIG. 9. Spatial location of total captures for *Peromyscus leucopus* on Grid II.

ping grids. In Grid II (burned) *P. leucopus* was caught most often at those stations in closest proximity to the neighboring forest (Fig. 9). This would seem to indicate that individuals of this species were foraging into the burned habitat from the nearby forest edge. Grid I (unburned 3 years) was also in close proximity to a forest edge (Fig. 1), yet there were only 2 captures of *P. leucopus* on this grid as opposed to 144 captures on Grid II. The most obvious difference between these grids was the presence or absence of litter.

There is some evidence that interspecific competition may be influencing the distribution of *Peromyscus* species. Figure 6 indicates a moderate but fairly stable population density for *P. maniculatus* on Grid III where *P. leucopus* is nearly absent. However, in Grid II where there was a significant number of *P. leucopus* individuals entering from the forest edge, there was a steady decline in *P. maniculatus* density.

Distribution of Other Species. Although caught in low numbers, *Z. hudsonius* definitely preferred the burned prairie. This preference for a clear understory and absence of litter probably reflects the special locomotor abilities of this very active and far-ranging rodent (Schramm 1970). In contrast, *R. megalotis* exhibited a wide habitat range, being caught in both burned and unburned grids during all stages of vegetational recovery. *B. brevicauda* preferred the unburned grids, particularly Grid I (unburned 3 years), which agrees with results from a previous study at the Knox field station (Springer and Schramm 1972) in which shrew densities did not return to pre-burn levels until 2½ years after burning. A preference for litter is probably due to the tendency of *B. brevicauda* to build tunnels through organic debris at the soil surface much like *Microtus* (Hoffmeister and Mohr 1972). In addition, removal of litter eliminates the moist microclimate that attracts the preferred foods of *B. brevicauda* such as earthworms, snails, and slugs (Whitaker and Ferraro 1963, Springer and Schramm 1972).

ACKNOWLEDGMENTS

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MAXTON PLAINS, PRAIRIE REFUGIA OF DRUMMOND ISLAND, CHIPPEWA COUNTY, MICHIGAN

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Abstract. Treeless areas totaling several hundreds of hectares on Drummond Island are dominated by grasses, sedges, and broad-leaved herbs, mostly with western or northern affinities. These sites, collectively known as the Maxton Plains, are underlain by dolomitic limestone and are largely devoid of glacial till. This study focuses on the composition and structure of the vegetation of 5 of the larger openings, and on the zone of encroachment by the surrounding forest communities. Results suggest that these openings have not been forested during Holocene time, and that the sites represent stable communities which are highly resistant to invasion by adjacent forest or introduced alien species.

INTRODUCTION

Natural grasslands occurring in the southern and central Lower Peninsula of Michigan (e.g., Gleason 1917, Hauser 1953, Scharrer 1971) have generally been considered to mark the northern boundary of the Prairie Peninsula (Transeau 1935) in the state. Although isolated populations of prairie species occur well north of the Prairie Peninsula, no natural grasslands have been recognized nor described from the northern portion of the state. This paper reports the results of a preliminary survey of a number of treeless communities, collectively known as the Maxton Plains, on Drummond Island, Chippewa Co., Michigan. Previous work on these communities has been confined to investigations of the flora of limestone "pavement" and outcrop communities (Hiltunen 1962) where a large number of plant taxa occur that are rare in Michigan. However, similar communities, to which the term "alvar" has been applied, have been described from geologically similar sites in Ontario, Canada (Catling, et al. 1975). These sites extend from Manitoulin Is., approximately 100 km east of Drummond Is., to the eastern portion of the province. Many of the taxa occurring on Drummond Is. also occur on 1 or more of the outcrop communities further east, albeit in differing combinations.

THE STUDY AREA

Drummond Island is located approximately 1 km east of the eastern tip of the Upper Peninsula of Michigan at the confluence of the St. Marys River system and the northern end of Lake Huron. Irregular in shape, the Island covers approximately 310 km², with extreme dimensions of ca. 32 km from east to west and 21 km from north to south.

The entire Island is underlain by Silurian age dolomitic limestone which outcrops frequently at scattered points, but which is largely free of glacial till over extensive areas of the Island's northern edge where the Maxton Plains study sites are located. The dominant vegetation on this portion of the Island is a mosaic of boreal forest patches dominated to varying degrees by *Picea glauca, Populus tremuloides, Thuja occidentalis* or *Abies balsamea* on well-drained sites, and *Thuja, Larix laricina, Populus balsamifera* and/or *Fraxinus nigra* on poorly drained sites. *Pinus resinosa* and *P. strobus* both occur sporadically, but at least the former appears to be largely restricted to small islands of till. The remainder of the Island supports a mixture of northern hardwoods and boreal forest. Witness tree records and notes from the original land survey, made by Mr. John Mullett in 1845, suggest that little has changed in the Maxton Plains area since that time.

In the study area, the treeless openings occur as a nearly continuous strip approximately 5.5 km in length, extending westward to the shore of Potagannissing Bay, and vary in width from a few to several hundred meters. Two large, more or less disjunct openings, in part man-made, lie approximately 1 km east of the long strip, and numerous smaller openings occur on either side of the long strip. Throughout this part of the Island the surface dips gradually from northwest to southeast, with slopes generally 1 percent or less. As a consequence, the southern (lower) edge of the openings grade into wetlands, and the northern (upper) edges grade into upland forest.

Climatic data (Michigan Department of Agriculture Weather Service, East Lansing, MI) for De Tour Village on the mainland, approximately 22 km straight-line distance west of the study area, show a mean annual temperature of 5.2°C (for the period 1970-81); January is the coldest month, with a mean temperature of −9.3°C; however, February has the lowest mean minimum temperature (−14.2°C). July is the warmest month with a mean temperature of 19°C and mean extremes of 24.8°C and 13.2°C. Mean annual precipitation for the period 1951-81 is 759 mm, of which 52% is received during the months of May through September. Snow is commonly permanent from late November to late March.

METHODS

Five sites, 2 with extensive dolomite exposure (D1 and D2) and three (Camp, Geum, and Aspen) with continuous vegetative cover, were chosen for a descriptive analysis of the grassland communities. Upper (dry) transitions were sampled at 4 of the sites, and lower (wet) transitions, at 3 of the sites.

Individual sample units consisted of a 10 × 10 m quadrat; herbaceous cover was estimated in 5 1-m² quadrats located randomly within the larger quadrat. Basal cover of the clonal taxa was estimated to the nearest 5% with the aid of a frame divided into 0.25-dm² units. Single occurrences or taxa with small amounts of cover were scored as present and assigned an arbitrary value of 1%. In transition and forest sites, stem numbers and diameters for each arborescent species, and crown diameters for each shrub species were determined over the entire 100 m² quadrat.

Soil depths were determined by probing each 1 m² sample quadrat in each corner and the center with a metal rod; these values were then averaged for the site. Three volumetric and batch soil samples were taken from each site on 26 June 1982 for soil density, moisture, organic matter, and *p*H determinations; these were sealed in plastic bags and held in the field in a cooler for transport to the laboratory in East Lansing, MI. Samples were dried at 100°C for soil moisture and density estimates, and subsamples combusted at 500°C for organic matter estimates; *p*H determinations were made within 4 days of collection using a mixture of 10 g of screened, undried soil in 100 ml of water.

Botanical nomenclature generally follows Voss (1972) for the monocots, and Fernald (1950) for the dicots, gymnosperms, and vascular cryptogams. Distribution of boreal taxa follows Hulten (1968). Statistical procedures follow Sokal and Rohlf (1969).

RESULTS

Treeless Sites

The treeless openings on Drummond Island range from sites with extensive exposures of bedrock (pavement sites) to those with essentially complete vegetation and soil cover

TABLE 1. Relative cover (%) of the major taxa in selected grassland sites; see text for explanation of site designations. Values are $\overline{X} \pm 1$ standard deviation.

SPECIES	D1-DRY	D2-DRY	CAMP-D	GEUM	ASPEN	D1-WET	D2-WET	CAMP-W
Sporobolus heterolepis	50 ± 23.0	48 ± 24.5	36 ± 32.1	72 ± 15.7	45 ± 20.4	56 ± 18.6	72 ± 20.9	70 ± 18.5
Schizachyrium scoparium	6 ± 10.5	3 ± 4.9		5 ± 13.2	32 ± 17.0		2 ± 2.3	
Geum triflorum		<0.1	<0.1	5 ± 11.0	7 ± 10.7			
Carex scirpoidea	24 ± 23.7	19 ± 14.6	<0.1	1 ± 2.1	<0.1	16 ± 12.4	4 ± 6.1	
Senecio pauperculus	2 ± 3.0	1 ± 1.3	7 ± 11.4	6 ± 6.1	2 ± 2.4	<0.1	<0.1	7 ± 8.2
Cerastium arvense	<0.1	<0.1	<0.1	<0.1	<1.0	<0.1	<0.1	
Comandra richardsiana	2 ± 3.0		<1.0		<1.0			
Fragaria virginiana	<0.1	<0.1	20 ± 20.9	<1.0		<0.1		<0.1
Agropyron caninum	<0.1	<0.1	<1.0		<1.0			
Achillea lanulosa				<1.0		<0.1	<0.1	7 ± 6.4
Carex crawei	<0.1	<0.1		2 ± 4.9	<0.1	<0.1	<0.1	1 ± 2.1
C. merritt-fernaldii			<0.1	<0.1	<0.1	<0.1		<0.1
Eleocharis compressa	<0.1	<0.1	33 ± 22.7	<0.1		13 ± 11.2	2 ± 3.0	6 ± 8.1
Ranunculus fascicularis	<0.1	<0.1	<1.0	<0.1	<1.0	<0.1	<0.1	<0.1
Saxifraga virginiensis		<0.1		<0.1		<0.1		<0.1
Poa compressa	<0.1	<1.0	<0.1	2 ± 1.6	<0.1	<0.1	1 ± 1.2	2 ± 2.7
Hieracium piloselloides	4 ± 9.2	1 ± 2.2	4 ± 3.7	4 ± 5.4	7 ± 6.0	<0.1	2 ± 2.4	3 ± 4.9
Hypericum perforatum		1 ± 2.4				<0.1	<0.1	2 ± 4.0
Total species in sample	28	27	15	18	21	16	12	13
Total ground cover	56 ± 12.9	45 ± 23.0	75 ± 13.4	88 ± 16.9	68 ± 12.5	59 ± 13.1	85 ± 13.7	84 ± 12.1

(grasslands). Except for the deeper depressions, in which ponding may occur, and at the extreme lower end of the drainage gradient, the dominant species throughout is *Sporobolus heterolepis* (Table 1). The only other grass of general occurrence which also plays an important role in mid-continental North American grasslands is *Schizachyrium scoparium* (= *Andropogon scoparius*), which is most abundant in the pavement sites and bordering the upland transition where forest encroachment is occurring. A somewhat similar distribution can be seen for the dioecious sedge *Carex scirpoidea*, which is most abundant in the drier sites but becomes localized and patchy under continuous cover conditions. Collectively, these 3 species contribute a major portion of the cover throughout all of the openings examined. Several graminoid taxa, e.g., *Agropyron caninum* (= *A. trachycaulum*), *Carex richardsonii*, *C. crawei*, *C. merritt-fernaldii*, and *Eleocharis compressa* are of general distribution, but of lesser importance in terms of cover contribution in most sites. *Sporobolus vaginiflorus* is of general occurrence in frost boils, dry pannes, and disturbed sites.

Among the more conspicuous forbs, *Geum triflorum* is the most disjunct from a generally mid-continental and western distribution, and it is apparently restricted to larger openings on the western side of the Island. *Senecio pauperculus* is the most generally distributed of the native forbs, occurring as widely scattered plants or as high-density patches (to several m²), the latter usually in shallow depressions. Other generally distributed and/or conspicuous native herbs include *Castilleja coccinea*, *Ranunculus fascicularis*, *Comandra richardsiana* and *Saxifraga virginiensis*. *Cerastium arvense* is common throughout the grassland sites, less frequent in the pavement sites. Two species, *Hieracium cf. pilosselloides* (*sensu* Voss and Böhlke 1978) and *Poa compressa*, widely accepted as introduced, are generally distributed throughout all sites. These and the less common alien, *Hypericum perforatum*, are never abundant except in disturbed soils along the road and associated drain channels. Several other introduced taxa which occur in the general area but were not recorded from the sample sites are worth noting; *Poa pratensis*, *Phleum pratense*, *Agropyron repens*, *Chrysanthemum leucanthemum*, *Hieracium aurantiacum*, and *Centaurea maculosa* are common and conspicuous elements of the roadside flora and where disturbance has occurred in the grassland, but have not successfully invaded undisturbed areas.

Four woody taxa are common throughout the grassland sites. *Juniperus horizontalis* is essentially restricted to exposed pavement sites, while *Amelanchier humilis* and *Prunus pumila* are of more general distribution. *Potentilla fruticosa* is most abundant at the lower end of the drainage gradient and dominates in some of the associated wetland sites (e.g., D1). Isolated seedlings of *Picea glauca*, *Juniperus communis*, and *Shepherdia canadensis* are widely scattered throughout all of the openings examined but apparently do not persist or do not become important elements of the vegetation beyond the forest-transition border.

Both the qualitative and quantitative properties of the grassland appear to be closely related to the position on the slope, especially in openings with extensive pavement, although the trend is toward greater absolute ground cover and dominance by *Sporobolus heterolepis* downslope in both pavement and grassland sites. Soil depths also tend to increase from upslope to downslope position; again, this is most conspicuous in pavement sites, whereas in grassland sites soil depths are essentially uniform (Table 2).

The soils are dark brown to nearly black, and contain only small amounts of sand—this presumably derived from the parent dolomite bedrock. Preliminary determinations indicate a range of ca. 15% to 35% organic matter (OM) in samples taken from beneath vegetation in both pavement and grassland sites; however these values may be inflated due to carbonate contributions from the dolomite. The relatively large OM fraction is reflected in the generally low soil densities (Table 2) and *p*H values which ranged from 6.1 to 6.9, in spite of the close association with basic bedrock. For comparison of soil densities, fine silica sand has an equivalent density of ca. 1.5 g cm^{-3}.

Soil moisture in June 1982, exhibited downslope increase in pavement sites (11-43%), but did not vary substantially with slope position within the grassland sites. In addition, the frequency and depth of fracturing of the dolomite appear to contribute to differential soil-vegetation development (although these aspects have not been thoroughly studied). Examination of the road and drain surfaces suggests that the bedrock in areas of lowest cover is more frequently and deeply fractured than in sites with continuous cover. A greater frequency of fractures may enhance surface drainage and thus contribute to drier conditions than in sites with fewer fractures. That these fractures are important in the hydrology of the system is reflected in wet streaks associated with them observed in the road beds during extended dry periods (e.g., June 1982). Weathering of the dolomite surface commonly results in a horizontally bedded, platey structure in pavement sites, whereas in sites with continuous cover, weathering results in a pebbly or cobbly surface at the soil-bedrock interface. These varying conditions may reflect differences in chemical composition or physical properties related to the original depositional environment; however, these variations may also be a result of, rather than a cause of differential vegetation development.

Forest and Transition Zones

Any interpretation of the origin and ecology of the grasslands, as well as future management strategies, must consider the forest and transition zones bordering or surrounding them.

As with the variations observed within the treeless communities, the effects of slope are of obvious importance in governing the nature of the transition. The lowland or wet transition zones present the least complex gradation from grassland to forest (or other stable) community. Here there are steep vegetation gradients, grading from *Sporobolus heterolepis* dominance, to *Carex* spp. and non-grassland forb dominance, to one of several lowland forest types, or mixed emergent and fen communities, within distances of 5 to 30 m. Soil substrate depth and, in general, soil moisture, increase continuously along the gradient, and encroachment into the grassland by transition zone species is slight.

In contrast, the upland transition zone is often broad and variable. *Populus tremuloides* is the most important invader, occurring either as a transitional band peripheral to the mature forest or as islands within the larger openings. *Juniperus communis, Picea glauca* and *Shepherdia canadensis* are also primary invaders locally, either singly or in combination, but are more important as secondary invaders beneath *Populus.*

Among the woody invaders, *Populus* appears to be the most effective in fractionating the grassland community and promoting decline of the dominants. Secondary invaders, including components of the mature boreal forest, become established behind the invading *Populus* front, increasing in density and plant size toward the older portions of the *Populus* stand. It is notable that most of these secondary invaders produce animal-dispersed fruits; demographic data suggest that prominent or isolated *Populus* may function as foci for the establishment of these species. For example, the distribution of *Shepherdia* within the *Populus* site demonstrated a significant relationship between *Populus* size ($\approx$ age) and the probability of *Shepherdia* occurring beneath the projected crown area (Fig. 1). Within the 70 × 40 m census area, the 146 *Populus* $\geq$ 4 cm basal diameter collectively produced ca. 54% canopy cover; of the 136 *Shepherdia* censused in the same area, 116 occurred beneath *Populus,* and 20 were not associated with a living tree. Of those associated with

TABLE 2. Mean ground cover values for the herb layer, soil depth, soil density, and soil moisture (26 June 1982) for upper and lower pavement and grassland transition sites.

SAMPLE LOCALITIES	TOTAL HERB COVER (%)	SOIL DEPTH (CM)	SOIL DENSITY*	SOIL MOISTURE (%)
Pavement sites				
(upper) Open	50.5 ± 18.0**	2.0 ± 0.9	0.83	11
Transition	45.8 ± 7.0	3.5 ± 2.7	0.55	13
Forest	36.5 ± 28.3	9.6 ± 5.0	0.26	50
(lower) Open	72.0 ± 13.0	6.2 ± 3.0	0.34	43
Transition	88.4 ± 4.1	11.2 ± 4.1	0.48	33
Forest-fen	89.1 ± 12.0	>30		
Grassland sites				
(upper) Open	77.2 ± 12.0	8.8 ± 5.9	0.34	47
Transition	71.2 ± 16.0	7.4 ± 6.1	0.30	46
Forest	30.0 ± 37.3	9.0 ± 3.4	0.30	33
(lower) Open	84.6 ± 12.7	9.2 ± 3.0	0.30	42
Transition	89.9 ± 9.0	18.6 ± 3.5	0.24	52
Forest	51.0 ± 27.5	21.3 ± 11.2	0.36	54

* g cm^{-3}

** estimates of dispersion are ± 1 standard deviation.

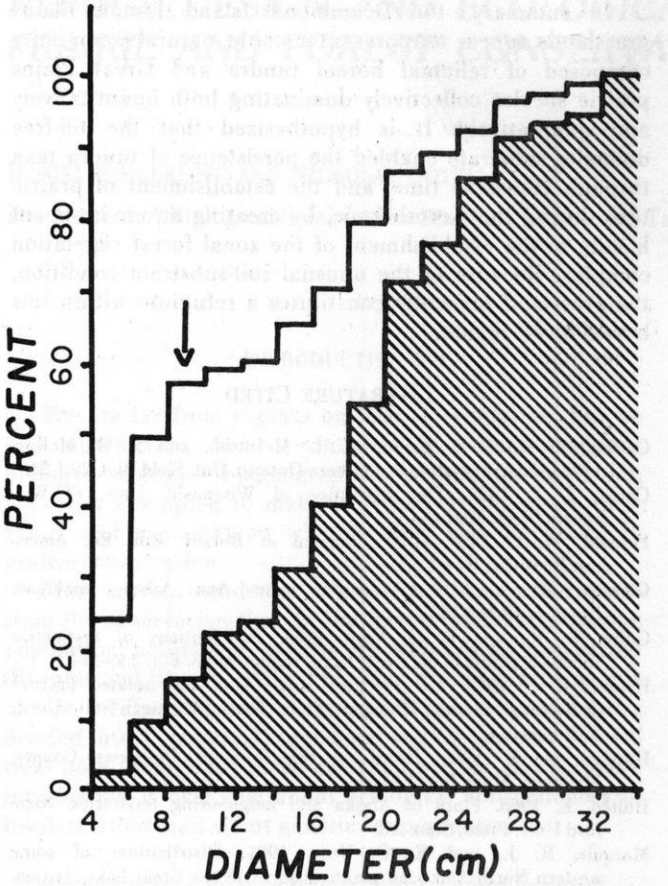

FIG. 1. Cumulative frequency curves showing size class structure of the *Populus* population (stems > 4 cm diameter) at the Aspen Island site: Upper (open) curve, all stems; lower (shaded) curve, trees associated with *Shepherdia.* Kolmogorov-Smirnov $d_{max.}$ (arrow) $= 0.408$, $\chi^2 = 30.9$, $P << 0.001$, indicates highly significant non-random association of *Shepherdia* with larger *Populus* size classes.

Populus, 67% occurred beneath trees $\geq$ 16 cm basal diameter (35% of the total *Populus* sampled). A similar, but less obvious, relationship was seen in *Juniperus* distribution; large, reproductive-sized individuals demonstrated the same distribution pattern as *Shepherdia.* However, a much larger number of individuals of smaller size classes, including seedlings, were generally distributed throughout the site.

The invasion process, either by *Populus* or gymnosperms, appears to be slow and perhaps sporadic. Mortality was found to be generally high in the smaller size class *Populus* sprouts at the invading front (ca. 38% standing dead); deer browsing was very apparent. Ring counts of *Picea* and *Juniperus* "seedlings" ranged from 9 to 16 at two sites (Geum and Camp) where the next larger size class of both species was reproductive individuals with 40 or more rings. One recently wind-thrown *Picea* with cones was 22 cm in diameter and had 62 rings at 1 m above ground level. The gap in size-age classes suggests that successful seedling establishment is episodic, and wholesale mortality probably occurs during drought periods, at least among the smaller size classes.

The extent of change in composition and structure of the herb layer across the transition zones is shown by coefficient of similarity (Sørensen's Index) values in Table 3. With the development of a mature forest or fen complex, the grassland flora is largely or completely replaced. These values also demonstrate the greater degree of change across the wet transition than across the dry transition.

TABLE 3. Sørensen's Index values, based on relative cover, showing similarity among herb layers of open, transition, and forest sites.

SAMPLE LOCALITY	OPEN-TRANSIT	OPEN-FOREST	TRANSIT-FOREST
Pavement (upper)	16.8	12.8	22.8
(lower)	9.9	<1	43.5
Grassland (upper)	46.3	3.7	39.6
(lower)	18.6	<1	8.1

DISCUSSION AND CONCLUSIONS

Several attributes of the Drummond Island-Maxton Plains pavement and grassland communities underscore their unique origin and formation in the upper Great Lakes region, as well as their potential for the study of community dynamics: (1) the rather unusual, if not unique, existence of previously unforested, natural, upland openings in a region where the zonal vegetation is forest, (2) the unique floristic composition of the pavement-grassland communities, with dominance by disjunct elements from disparate formations, and (3) the contiguity of 2 stable or climax communities of contrasting physiognomy, the distribution of which are unrelated to any apparent environmental discontinuities.

The conclusion that the Maxton Plains pavement and grassland communities have never been forested is largely inferential. That they are not post-settlement artifacts is shown by the original survey records. However, the contention that the openings were not forested sometime during Holocene time, e.g., prior to the Xerothermic, is supported by the primary seral nature of the herbaceous pavement communities, with the grasslands interpreted as the endpoint of that seral sequence. Just as Curtis (1959:362-3) depicted the fens of Wisconsin as "hybrid communities" consisting of floristic elements sorted from each of the major formations as they passed through during post-glacial time, the contemporary areas and affinities of much of the pavement and grassland flora suggests a hybrid origin. Two major elements contribute most of the vegetative cover; (1) an arctic and/or boreal-cordilleran, exemplified by the circumpolar *Carex scirpoidea,* and *Cerastium arvense, Senecio pauperculus, Agropyron caninum, Achillea lanulosa, Aster ptarmicoides, Primula mistassinica, Deschampsia caespitosa, Trisetum spicatum,* and the *Saxifraga virginiensis-S. nivalis* complex, and (2) a mid-continental element exemplified by *Sporobolus heterolepis* and *Schizachyrium scoparium* among the co-dominants, and other taxa such as *Geum triflorum, Ranunculus fascicularis, Sporobolus vaginiflorus,* and several *Carex* spp. A third, and quantitatively less important element, is composed of a generally more southern or eastern element exemplified by *Eleocharis compressa* and *Dichanthelium acuminatum.*

Schuster (1953, 1957) has drawn attention to the "tundra-like" zone bordering portions of Lake Superior, citing similarities in physiognomy and floristic composition of these shoreline communities to those occurring in arctic and alpine tundra. Guire and Voss (1963), Marquis and Voss (1981), and Soper et al. (1965) discuss the occurrence of many distinctive Great Lakes shoreline plants, including western and boreal disjuncts. Many of these taxa are calciphiles or saxicoles, as are a majority of the Drummond Island pavement and grassland species, and represent remnants of a once more extensive flora which followed closely the receding glaciers northward during the Holocene. All but the most drought- and heat-tolerant elements must have been eliminated during the Xerothermic, leaving a community open to invasion by the contemporary prairie dominants. This latter group may well have invaded via the shoreline habitat, in which prairie species frequently occur further south. Palynological studies may shed light on the timing of entry of the prairie element into the Drummond Island communities.

The stability of the grasslands (i.e., their resistance to establishment by either forest-transition or introduced species) is evident in the current patterns of invasion. Encroachment by forest is primarily peripheral, and the population structure of invading woody taxa suggest either or both episodic and catastrophic mortality in these taxa at the grassland-forest interface. Further study is needed to clarify aspects of both the nature and rate of encroachment. Certainly the effects of browsing deer are important at the present time, as evidence by the prominent browse line observable throughout the transition. Similarly, the successful establishment of alien taxa appears to be strongly dependent on man-made disturbance or natural physical instability of the environment. For example, most of the common ruderal taxa are confined to the road corridor which transects the openings. Here, increased soil depth and disturbance from periodic maintenance operations appear to be responsible for either or both the introduction and maintenance of "weed" populations. Exceptions to this are the widespread *Poa compressa*, *Hieracium piloselloides*, and *Hypericum perforatum*; curiously, these species were not observed to form extensive or dense patches as they frequently do in secondary successional sites further south and west—rather, they appear to behave as native, subordinate taxa. Elsewhere, the interface between grassland-pavement communities and the lowland transition appears to be more subject to invasion, perhaps as the result of annual or longer term fluctuations in water levels maintaining the communities in a state of flux.

In summary, the Drummond Island-Maxton Plains grasslands appear to represent a stable, natural community composed of relictual boreal tundra and Great Plains prairie species collectively dominating both quantitatively and qualitatively. It is hypothesized that the till-free dolomite substrate enabled the persistence of tundra taxa through Holocene time, and the establishment of prairie taxa during the Xerothermic, by creating an environment hostile to the establishment of the zonal forest vegetation complex. Because of the unusual soil-substrate condition, the grassland presently constitutes a refugium within this boreal forest region.

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REFUGE DESIGN AND ECOLOGICAL THEORY: LESSONS FOR PRAIRIE AND FOREST CONSERVATION[1]

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INTRODUCTION

We are far from experts on prairie vegetation, but we can summarize some contributions that academic biology—ecology, biogeography, population genetics, etc.—has attempted to make to conservation, assess their value, and comment on whether they may be useful in prairie conservation.

Most current academic interest in conservation stems from the observation that, in the face of increasing human population, habitats of all sorts are increasingly insularized (Burgess and Sharpe 1981). This is as true of prairie as it is of forest. Effects of this insularization can conveniently be divided into 2 classes: (1) ecological and (2) genetic. We will treat both, though far more has been written and far more information is available about ecological consequences of insularization than about genetic consequences.

ECOLOGICAL AND BIOGEOGRAPHIC CONSIDERATIONS

The Species-area Relationship

One of ecology's oldest generalizations is the "species-area relationship," that large areas or islands tend to have more species of organisms than do small ones (Connor and McCoy 1979). Prairie data (e.g., Fig. 1) clearly depict this tendency (Glass 1981). Here we plot species lists, kindly provided by William Glass, of goldenrods, milkweeds, and legumes in 56 prairie fragments of different sizes in Iowa and Minnesota. These prairies consisted of all unplowed patches on the terminal glacial moraine that contained big and little bluestem and were not grazed to the point that *Amorpha canescens* was absent. It is apparent that bigger prairies have more species of all 3 plant groups total, or of any 1 of them like goldenrods, than do smaller prairies, and the statistics of the regressions bear this out (Glass 1981). Consequently it appears that if 2 prairie fragments are identical in every way (e.g., habitat diversity, cost, etc.) except for area, the larger 1 would make the better refuge if the goal is to conserve as many species as possible.

At the outset we should qualify 2 aspects of this statement. First, it is far from clear that the usual conservation goal is to conserve the most species (Simberloff and Abele 1982). Academic ecologists take this goal as given (e.g., Cole 1981, p. 631), but to us it seems that conservationists at least as frequently articulate a very different aim—to conserve certain species of particular interest. A prairie fan, for example, might say to hell with *Solidago rigida* and *Asclepias syriaca* and principles derived from their distributions—he/she cares only about genuine prairie plants like *S. riddellii* and *A sullivantii*! Second, conservation can never be forever. Paleontology tells us that no species is immortal. For example, of all animal species that have ever existed, at least 99% are extinct (Moore et al. 1952), and even though the rate of extinction has vastly accelerated because of recent human activity (Simberloff 1982a), most extinctions were in the geologic past and were not anthropogenous. Environments change, chance catastrophes occur, evolution proceeds, and every species is doomed to extinction sooner or later. The best we conservationists can hope to achieve by enlightened management practices is to defer the inevitable extinction. So when we say that a larger refuge is better than an otherwise identical but smaller one, we mean that the rate of extinction in the community is slower or, for a single species, that the expected time to extinction is longer.

Island Biogeographic Theory and the One-Large-vs.-Many-Small Debate

Granted that a single large refuge is likely better than an otherwise equivalent single small refuge, a major controversy has recently arisen over a related question. Given a certain area (say 40 acres) to be set aside for conservation, is it better strategy for it to be deployed as several small refuges (say 4 of 10 acres each) or 1 large one? Again, one may ask (a) which configuration conserves the most species and (b) which is likely to defer the extinction of any particular species the longest. It is surprising that most authors have followed the lead of Wilson and Willis (1975) in espousing the single large refuge over the cluster of smaller ones for both goals (a) and (b), arguing that the equilibrium theory of island biogeography (MacArthur and Wilson 1967) provides theoretical justification for such a choice. The theory views the biota of an island (or insular habitat such as a refuge) as a dynamic equilibrium, with a more or less constant number of species maintained by a balance between local extinction of resident species and immigration of new ones. What is surprising about application of the island theory in this conservation context is that:

(1) The theory itself has come under increasing criticism and has been shown to be at best an accurate depiction of only a few ecological communities (F. Gilbert 1980, Simberloff 1982b).

(2) It was quickly demonstrated that the theory, whatever its merits in other settings, offers no prediction about whether 1 large or several small

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[1] Presented as the featured address at the biennial banquet, 3 August 1982.

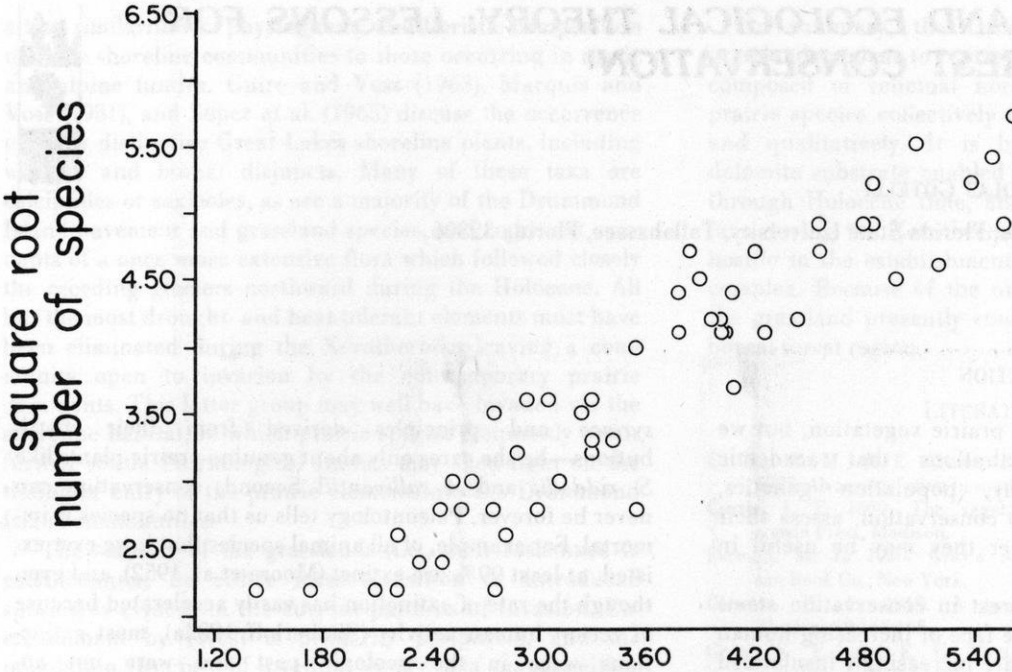

FIG. 1. Number of species of goldenrods, milkweeds, and legumes in 56 prairies studied by Glass (1981).

refuges is optimal (Simberloff and Abele 1976a, b, 1982; Higgs 1981).

(3) The few published data relevant to the issue show that, for a variety of taxa, habitats, and regions, several small sites generally support as many species as 1 large site, or even more species (Simberloff 1982a, Simberloff and Abele 1982).

The reason why the pattern cited in (3) obtains—why several small sites usually have at least as many species as 1 big one, and often have more—is discussed below. For now we are interested in whether prairie plants adhere to this pattern. Using the Glass data on milkweeds, goldenrods, and legumes, we found that they do. We randomly lumped together samples of pairs of Glass's prairies, trios, quartets, and so on up to groups of 10 prairies. Each prairie was assigned a number, and numbers were then drawn randomly. None of these simulated groups exceeded in area the largest of the single prairies. For each group of prairies, we amassed a list of all species present in the group. If we now regress number of species on area for single prairies, then pairs, trios, etc., we find (Figs. 2 and 3) that for a given area, on average, there are slightly but significantly more species the more separate refuges comprise the area. With area the first independent variable, number of patches still contributes significantly to species richness ($F = 45$, $P < 0.001$). That is, prairie plants of these 3 groups seem to behave like a number of other taxa: at least over the size range of the prairies Glass studied, groups of small prairies have slightly more species than 1 larger prairie of equal total area. Table 1 lists several such comparisons. Glass (1981, Table 2) gives 2 other comparisons that tend in the same direction. We have no data on whether groups of smaller sites differ from single large ones in any way other than contiguity, but Glass (pers. comm.) feels there are no apparent consistent physical differences between his small and his large sites.

TABLE 1. Six comparisons of species richness in single large prairies with that in groups of smaller ones, where total area is approximately equal. Data from Glass (1981).

Single Prairie		Multiple Prairies		
Area (m²)	Number of species	Number of species	Σ Area (m²)	Number of patches
660	7	11	587	3
957	8	14	920	3
3,290	16	16	3,217	2
17,500	17	22	17,485	8
34,729	24	28	32,025	2
960,000	23	31	930,615	8

This may all be well and good, but if there are certain key species absolutely restricted to large prairies, we still might opt for single large refuges over groups of smaller ones. One way this question is typically addressed is by looking to see what is the minimum size of island occupied by each species (references in Simberloff and Abele 1982). Glass (1981) uses his data exactly this way to conclude that legumes and milkweeds can survive in even his smallest prairie (5.7 m²), but that goldenrods may have difficulty maintaining their populations in prairies smaller than 50 m². We ordered Glass's 56 prairies from smallest to largest,

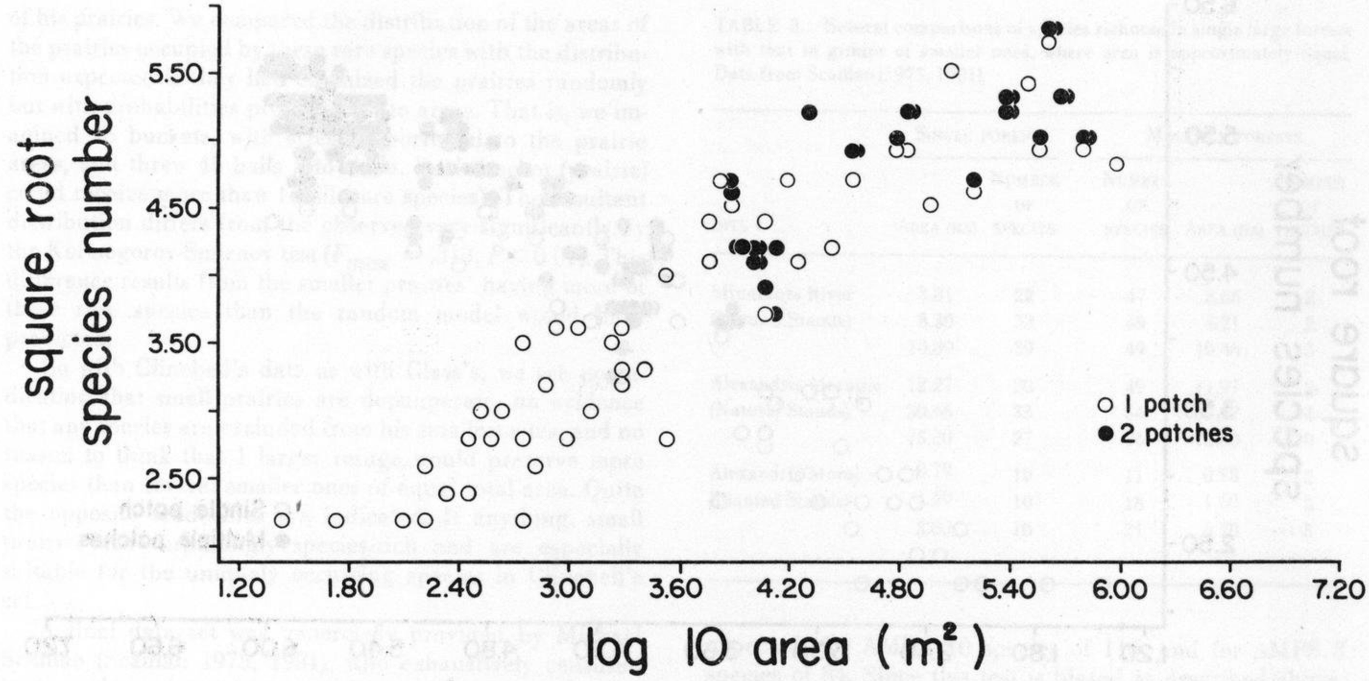

FIG. 2. Number of species of goldenrods, milkweeds, and legumes in single prairies and in groups composed of 2 randomly drawn prairies. Data from Glass (1981).

then for each of his 39 species found the rank L_i of the smallest prairie it inhabited. We then asked for each species i, if there were 56 buckets in a row (representing lowest rank on left and highest on right) and we randomly distributed its N_i occurrences among the 56 buckets, such that no 2 occurrences fall in the same bucket, what is the null probability that the left-most occurrence would have been even smaller than that observed (L_i). This probability is

$$1 - \frac{\begin{bmatrix} 56 - L_i + 1 \\ N_i \end{bmatrix}}{\begin{bmatrix} 56 \\ N_i \end{bmatrix}}$$

and for 23 of the 39 species this probability is greater than 5%. That is, it appears that almost half the species are avoiding small prairies.

However, this minimum-inhabited-size approach neglects the species-area relationship. Since small prairies have fewer species, we would have expected rather few species in the smallest. It is as if the buckets are not of equal size, but rather the left-most ones are smaller and the size increases to the right. We constructed 2 models of random colonization that account for the species-area relationship. First, for Glass's data, we divided the prairies into 3 size classes: small = < 1,000 m², intermediate = 1,000-12,000 m², large = > 12,000 m². We then asked, for each of his 39 plant species, how many of the prairies in each size class did it occupy? Of course smaller prairies have fewer species, as we pointed out above in discussing species-area curves. But a χ^2 contingency test showed that these species as a group do not "avoid" smaller prairies above and beyond the usual species-area effect. In fact, only 1 species, *Amorpha canescens*, of the 39 differs from the expected, given the marginal totals of how many species are found in each prairie and how many prairies each species occupies. That species tends to be found disproportionately in the smaller prairies.

Second, we constructed a mechanistic model of how a species i might come to occupy the sites that Glass observed, in order to examine the notion that at least some species "avoid" small prairies. We again considered 56 buckets, only this time they were different sizes, each bucket's size being proportional to the area of 1 of the prairies. For each species i, we simulated (by computer) throwing balls (representing propagules of the species) into the buckets until N_i of the buckets were occupied. That is, for every ball, the probability that it falls in bucket j is proportional to the size of bucket j. The N_i occupied buckets at the end of the simulation represent the occupied prairies. Having thus distributed each species' occurrences randomly among the appropriate number of prairies 10 times, we then compared, for each species, the observed areas of occupied prairies with the simulated expected areas by a Kolmogorov-Smirnov test. For only 1 species was there a significant difference ($P < .05$) between observed and expected. By chance alone, even if no species were avoiding small prairies, we would have expected about 2 species ($\approx .05 \times 39$) to show a significant difference. Once again we find no evidence that any species seem to avoid the small prairies.

Finally, we asked if Glass's small prairies tend to be depauperate in species. The model of the previous paragraph suggests not. To estimate the expected number of species $E(S_j)$ for prairie j, we simply summed the simulated probabilities, over all species i, that prairie j contains species i. The variance for each species is the binominal variance, and the variance for each prairie is simply the sum of the variances over all species. When we compare S_j to $E(S_j)$ we see that 25 of 56 prairies differ significantly from the expected species richness (14 > exp, 11 < exp), and the biggest differences are that a good fraction of the small prairies have more species than they should and that the large ones have fewer. All in all, for

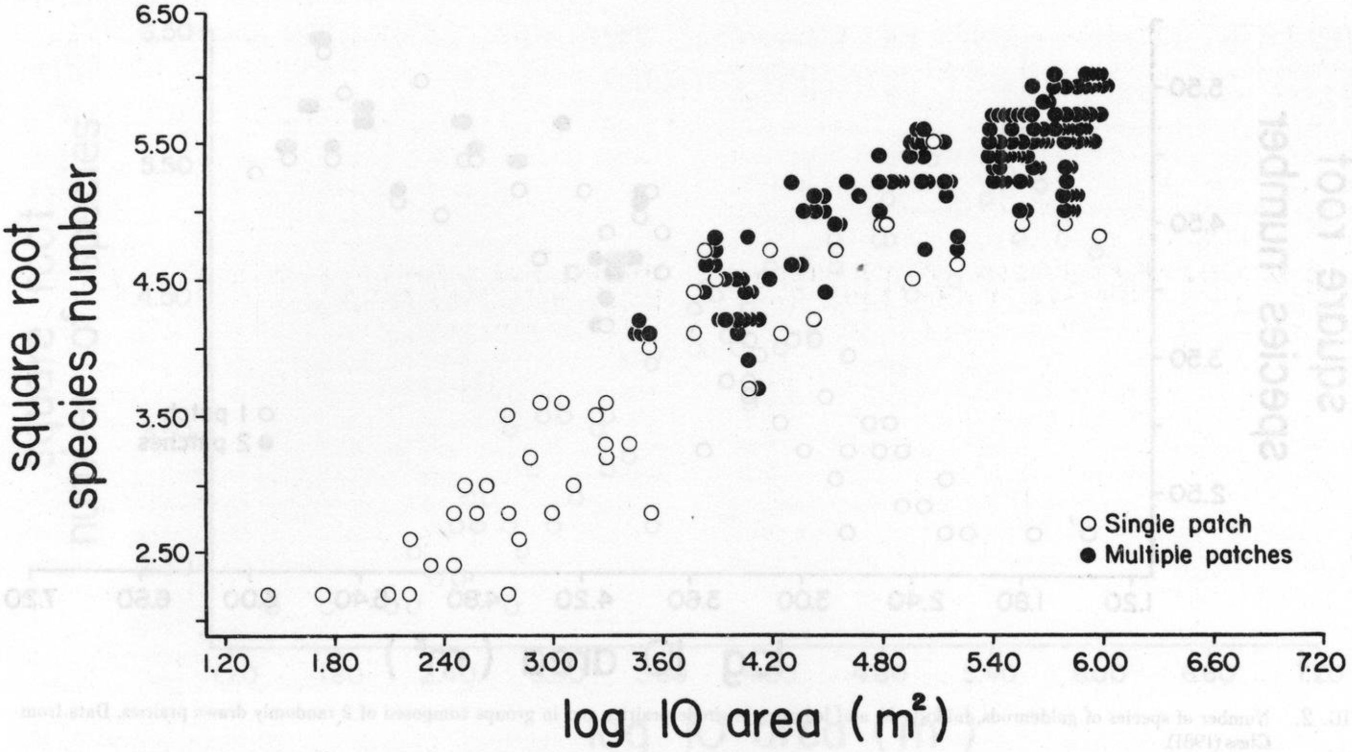

FIG. 3. Number of species of goldenrods, milkweeds, and legumes in single prairies and in groups composed of 2-10 randomly drawn prairies. Data from Glass (1981).

Glass's 3 plant groups, and over the size range of prairies he censused, there is absolutely no evidence that small prairies have surprisingly few species, that any species are excluded from small prairies, or that 1 larger prairie would be a better refuge than several small ones. If anything, the data show that a group of small prairies would likely contain more species than 1 large one, if total areas were equal.

A second data set, of all 152 angiosperm species on 15 prairies of varying size in Illinois, was kindly provided by Richard Clinebell, and allowed us to see whether the patterns we found for Glass's prairies obtain for a different data set. Once again (Fig. 4) there is a dominating species-area relationship ($R^2 = .567$, $P < .01$). As for Glass's data, we combined random sets of Clinebell's prairies (up to 5 prairies per set), and we found again that for a given area, on average, there are significantly more species the more separate prairies comprise the area. With area the first independent variable number of prairies still contributes significantly to species richness ($F = 14.7$, $P = .001$). In fact, for Clinebell's data, adding the number of prairies as a variable effects a major improvement in the regression, increasing R^2 by .09.

Even using a model where prairie area is not taken into account (the row of equal-size buckets described above), we find only 5 of the 152 species have their smallest prairie larger than uniform random assignments would have predicted (see above description for formula). So there is no evidence that Clinebell's species avoid small prairies, even with a model biased to show that they do. When we randomly distribute the N_i occurrences of each species into prairies according to area (see model above—unequal buckets) we find that only 1 of the 152 observed occurrence patterns differed significantly by Kolmogorov-Smirnov test from the expected (derived by 10 simulations). The result is exactly as with Glass's plants. Finally, if we ask, as we did with the Iowa prairies, whether small Illinois prairies tend to be impoverished in species beyond what we would have expected from area alone, we find (see model above) that observed number of species, S_j, differs from its expectation $E(S_j)$ in 9 of the 15 sites. The pattern of these differences is exactly as earlier: small prairies tend to have too many species and larger ones too few.

Finally, we analyzed a subset of Clinebell's plants separately. Of his 152 species, 45 are each found on only 1

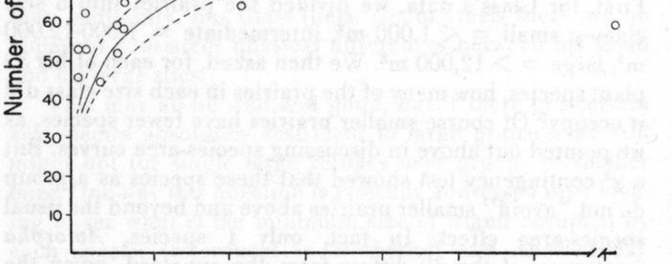

FIG. 4. Species-area curve for Illinois prairies studied by Clinebell, with best-fit curve and confidence limits (2 standard deviations from curve).

of his prairies. We compared the distribution of the areas of the prairies occupied by these rare species with the distribution expected if they had colonized the prairies randomly but with probabilities proportional to areas. That is, we imagined 15 buckets, with sizes proportional to the prairie areas, and threw 45 balls into them. Each bucket (prairie) could receive more than 1 ball (rare species). The resultant distribution differs from the observed very significantly by the Kolmogorov-Smirnov test ($F_{max} = .313, P < 0.01$). This difference results from the smaller prairies' having more of these rare species than the random model would have predicted.

So with Clinebell's data as with Glass's, we see no indication that small prairies are depauperate, no evidence that any species are excluded from his smallest sites, and no reason to think that 1 larger refuge would preserve more species than several smaller ones of equal total area. Quite the opposite tendencies are indicated. If anything, small prairies are surprisingly species-rich and are especially suitable for the uniquely occurring species in Clinebell's set.

A final data set was generously provided by Michael Scanlan (Scanlan 1975, 1981), who exhaustively censused herbs in the understory of many forest patches embedded in the west-central Minnesota prairies. Of several such groups of forests that Scanlan examined, we treat 3 here:

(1) The Minnesota River Tract (MRT)—12 remnants containing 102 species.

(2) The Alexandria Moraine Natural Sites (AMNS)—22 remnants containing 116 species.

(3) The Alexandria Moraine Planted Stands (AMPS)—43 planted forests containing 84 species.

All of Scanlan's groups adhere to the usual species-area relationships, and he also sought correlations between species richness and other variables, such as isolation (Scanlan, 1975, 1982).

We further subjected his data from the above 3 groups to the same sorts of analyses performed on Glass's and Clinebell's prarie data. First we combined random sets of forests (up to 4 for MRT, 10 for AMNS, and 5 for AMPS) to see whether 1 large or several small forests contained more species, on average. In all 3 groups, as with the Glass and Clinebell data, it was the latter. With area as the first independent variable, number of forests still increases species richness significantly (Table 2). Table 3 lists several specific comparisons for each group.

When we use the model of a row of equal buckets (area not taken into account) to see if species are excluded from small forests, we find for the MRT group only 1 of 102 species with a minimum forest size significantly larger than expected, for AMNS 10 species of 116, and for AMPS 8 species of 84. Since this test is biased as described above, we conclude that there is no evidence of exclusion from small forests. When we randomly distribute the N_i occurrences of each species into forests according to forest area (unequal bucket model), we find for the MRT group (10 simulations for expected) that none of the 102 species has a distribution of forest sizes significantly different ($P < .05$) from expected, by the Kolmogorov-Smirnov test. For the AMNS and AMPS group (10 simulations each) we find only 2 species in the AMNS group differing at the 5% level from expected, but 7 such species in the AMPS group. We would have to find about 5 such species in each group (ca. 5%) to reject the hypothesis of random assignment. If we use the same model as we did for the Glass and Clinebell data to see if small forests are species-depauperate, we find exactly the same result: they tend, if anything, to have too *many* species given their area, while large forests tend to have too few. For the MRT group one finds the expected number of species differs significantly from that observed in 9 of 12 forests; for the AMNS forests the comparable figure is 14 of 22, and for the AMPS sites it is 19 of 43. For all 3 groups it is the small forests that are too speciose.

TABLE 2. Effect of number of islands on species richness for herbs of 3 groups of forests (data from Scanlan 1975, 1981).

Forest group	Increase in R^2	F	Pr
MRT	.280	24.04	< .001
AMNS	.106	27.90	< .001
AMPS	.110	14.52	< .001

TABLE 3. Several comparisons of species richness in single large forests with that in groups of smaller ones, where area is approximately equal. Data from Scanlan (1975, 1981).

	Single forest		Multiple forests		
Site	Area (ha)	Number of species	Number of species	Area (ha)	Number of patches
Minnesota River	3.81	22	47	3.65	2
(Natural Stands)	8.30	32	49	8.21	2
	10.89	39	49	10.46	3
Alexandria Moraine	12.27	20	49	11.97	2
(Natural Stands)	30.66	33	54	30.67	4
	75.20	27	76	73.60	9
Alexandria Moraine	0.79	10	11	0.78	2
(Planted Stands)	1.60	10	18	1.60	3
	3.80	16	21	3.78	3

Finally, when we look at "rare" species (those found in only 1 forest) in all 3 forest groups exactly as we did for Clinebell's prairie plants, we find the same result (Table 4): a disproportionately large number of these species occur in *small* forests.

TABLE 4. Kolmogorov-Smirnov statistics for distribution of "rare" herbs in 3 groups of forests (data from Scanlan 1975, 1981).

Forest group	Total species	"Rare" species	F_{MAX}	P
MRT	102	36	.301	< .01
AMNS	116	31	.395	< .01
AMPS	84	36	.267	< .05

Habitat Diversity

We thus see for data on 2 sets of prairie plants and 3 sets of forest herbs a recurrent pattern: no species are excluded from small refuges, and groups of small refuges tend to have a few more species than do single larger refuges of equal total area. This same tendency has been seen in a variety of other taxa (Simberloff 1982a). Among plants it has been noted by Game and Peterken (1981) for woodland herbs, Higgs and Usher (1980) for plants of Yorkshire limestone pavements, chalk quarry reserves, lowland heaths, and Scottish soft coastal habitats, Malyshev (1980) for plants of large regions, and Järvinen (1982) for woodland angiosperms in the Åland Islands. A likely explanation for this tendency resides in what is probably ecology's oldest and firmest generalization: each species is restricted to a range of habitats or microhabitats, and species differ in their optimal habitats. In fact, the most common explanation for the species-area relationship has traditionally been that larger areas have, on average, more habitats, and therefore have more species (Connor and McCoy 1979). Even though other forces may contribute to the increase in species richness with area (Simberloff 1976), habitat diversity must usually be the most important variable. It is reasonable to hypothesize, then, that on average a group of distinct refuges, simply by virtue of spatial separation, will encompass a greater variety of habitats than will a single refuge of equal total area. Game and Peterken (1981) propose exactly this explanation for their woodland herb results: a random collection of small woods would likely have more habitats than 1 large one would. They add that, if one set out to maximize habitat diversity, one could exaggerate the advantages of a group of small refuges by choosing diverse and unusual habitats. A similar conclusion was reached by Kitchener et al. (1980) for lizards of the Autralian wheatbelt:

> . . . while scattered small reserves, totalling 1.78 × 10^4 ha, contain almost all known lizard species in the . . . wheatbelt, a single area . . . in order to contain the same number of species would need to be immensely larger—possibly by a factor of 600. This situation is again believed to reflect the heterogeneity of habitat within the region such that an enormous area is required to encompass all its habitat diversity and consequently to carry representatives of all lizard species in the region.

But there is a problem with our explanation of increased species richness on groups of small sites by virtue of increased habitat diversity: so far it is only a plausible story. In fact, even if all botanists would agree that each plant has species-specific habitat requirements, very rarely have these been precisely specified. Rabinowitz (1981) points out that many rare plants are rare because their required habitat is rare—*Solidago bartramiana* is an example. But for every plant that has been sufficiently studied to allow us to attribute rarity to habitat specificity there are dozens of rare plants where we are currently only guessing. In the prairie this situation obtains *a fortiori,* though precise explanations for rarity are beginning to appear for some species (e.g., Rabinowitz 1978, Rabinowitz and Rapp 1981). Platt (1975, Platt and Weis 1977, Werner and Platt 1976) has focused on differences between coexisting species, though he has been more concerned with what permits coexistence between species of similar habitat than with what habitat restrictions could make species rare or absent.

As a start in demonstrating the role of habitat diversity in maintaining prairie plant species diversity, we used a data set from the Konza Prairie supplied by L. Hulbert. Four hundred thirty-two 10-m^2 quadrats were exhaustively censused, to see not only which plants were present but how abundant they were (7 classes). Further, the soil type is known for each quadrat; there are 7 different types represented. Johnson and Simberloff (1974) and Game and Peterken (1981) have shown that number of different soil types correlates highly significantly with number of plant species over groups of sites, although it is not possible to say for these data whether the soils are directly determining which plants are where (Simberloff 1982c). There is also a literature showing that some plants are restricted to certain soils (references in Simberloff 1982c) but this also need not imply a strong role for soil type diversity in maintaining plant species diversity. For the Konza plants there were also various burning and mowing regimes and various periods and seasons for these disturbances. We know that such disturbances are critical habitat variables for many prairie plants (Hulbert 1969, Hover and Bragg 1981), perhaps as critical as soil type. But the records of disturbance are not yet available in computerized form, so we were able to treat only soil type.

For each of the 168 species, we found how many of the 432 quadrats it occupied. We then constructed, for each species, a 7 × 2 χ^2 contingency table, with rows as soil types and columns as presence or absence, to test whether the presences and absences in the quadrats of different soil type were independent of soil type. That is, does each species tend to be present in or absent from certain soil types disproportionately, given its total number of occurrences? The results are clear-cut: Only 36 species showed no significant deviation from expected given random occurrence in quadrats of different soil types. Four species showed significant deviations in the contingency table as a whole, but these could not be assigned to preference or avoidance of any particular soils. The remaining 128 species all deviated significantly from expected and the deviation resulted from extraordinary positive or negative association with 1 or more soil types. The data, in sum, support Hulbert's contention (pers. comm.) that a practised prairie worker could usually tell the type of soil in a quadrat from a list of the plants present. One must conclude, then, that to conserve a given species or set of them, one must have the appropriate soil. Surely a similar conclusion would arise from an analysis of other habitat data if these were available.

We also find for the Clinebell prairie data and Scanlan forest herb data that species that are rare (or at least have small geographic ranges in these regions; Rabinowitz (1981) discusses what is meant by a "rare" species) tend to be found more frequently in the smallest sites than one would have expected if species were assigned randomly to sites on the basis of areas. And larger sites tend to have too few of these "rare" species. Why this pattern exists we cannot guess, unless it is simply a manifestation of the tendency we found in all the data sets we examined for small sites to have too many species and larger sites to have too few relative to random expectations. That is, it may be that "rare" plants (rare in this sense, anyway) are not distributed differently according to site size than are other plants. In any event, the conservation message is clear: this result reinforces our conclusion that groups of small refuges may be better than single larger ones. Järvinen (1982) also found that more "endangered" vascular plant species in the Åland Islands tend to be found in groups of small islands than on single large ones.

W. Platt (pers. comm.) has observed that the goldenrods, milkweeds, and legumes of Glass's (1981) study encompass a number of "weedy" species that are not "good" prairie plants and are especially suited to survival in small sites, and further that many of Glass's prairie sites exist today precisely because of their unusual habitats—stony or odd soil, severe slope, etc. Consequently he cautions that results from Glass's data might inordinately favor groups of small refuges and might not be valid for prairie plants as a whole. It is similarly true that Clinebell's small prairies include a number that likely have aberrant physical habitats, though Clinebell studied all species. Clinebell's and Scanlan's species lists do not include particularly large proportions of "weedy" species. Platt is correct to be cautious here, but at least Glass and Clinebell have data that can be brought to bear on conservation questions; even if the data sets are not the best ones conceivable for this purpose, they are the best there are. Although Platt's supposition that these sites may have aberrant habitats is reasonable, it is certainly not demonstrated. Nor, to our knowledge, have the exact habitat requirements of prairie plants been systematically determined, so we are not in a position at this time to discount lessons from the Glass and Clinebell studies.

That the prairie sites we have treated have unusual habitats may well exaggerate the expected increase in habitat diversity for groups of small sites compared to single large ones, although we have no data to test this. Similarly, that Glass's prairies are spread over such a large region means that our random subsets of them were especially likely to encompass substantial habitat diversity. In general, one might predict that the greater the distances among the small sites in a group, the larger the increase in number of species over that contained in a single, even large, site.

Insularization, Minimum Areas, and Species Loss

Much of the literature arguing against single small refuges or even groups of them (e.g., Terborgh 1974, Diamond 1975) stems from an observation plus a largely untested model that extends the observation. The observation is that, all other things being equal, an island usually has fewer species of any taxon than does an equal-sized quadrat on the mainland (MacArthur and Wilson 1967). One may always question whether 2 habitats are really equivalent, but if we take the observation at its face value, the standard explanation is that all species on the island must maintain their populations only on the island, while species in the quadrat may include several that are partially maintained in the surrounding matrix and only partially in the quadrat and others that are actually maintained in the surrounding matrix (say, because of a unique habitat there) and are only transients, albeit common ones, in the quadrat (MacArthur and Wilson 1967).

This explanation, in turn, is extended to imply that, when a hitherto continuous land mass is broken into patches or islands by either rising sea levels or anthropogenous destruction of vegetation, the islands will lose species and eventually come to a new, lower equilibrium. They do so because the same patch of land as an island can support fewer species than it does as a part of a larger contiguous land mass. The decline in species richness, though plausible, has to our knowledge been directly observed only once (Simberloff 1976), for insects on 3 very small mangrove islands, where a drop of ca. 12% to a new equilibrium was observed over 7 months. A second widely cited example, the avifauna of Barro Colorado Island (formed during the construction of the Panama Canal), is inappropriate since much of the island has undergone drastic habitat change since its formation (Simberloff and Abele 1976b). No other study records the number of species originally present on an island, but 3 authors (Diamond (1972) for New Guinea satellite island birds, Terborgh (1974, 1975) for West Indian birds, and Wilcox (1978) for reptiles of Gulf of California islands) have estimated numbers of species present before the late Pleistocene sea level rise and thus inferred the subsequent decline to present numbers. The estimates and/or courses of sea level rise are questionable in all 3 instances, however (Abele and Connor 1979, Faeth and Connor 1979). Fossil evidence can occasionally demonstrate an extinction, but cannot show whether species richness declined since it cannot indicate which species were originally present. Whitcomb et al. (1981) hypothesize a decline in avifaunal richness in eastern deciduous forest, but do not estimate how many species were originally present or document any actual local extinctions. On a larger scale, by World War II less than 1% of eastern virgin forest remained in the U.S., but this severe fragmentation has so far resulted in the extinction of at most 2 bird species, the Carolina parakeet and the ivory-billed woodpecker (Terborgh 1975). For his prairie plants, Glass (1981) concludes, on comparing species-area relations of isolated remnants with those of quadrats in larger prairies, that no species number decline has occurred, and some of his remnants are a century old. Game and Peterken (1981) use the same method on herbs of Lincolnshire forests, some of which are centuries old, and reach the same conclusion: even in woods of just a few hectares, species loss, if it occurs at all, is extremely slow.

So it is far from clear that a decline in species number automatically follows habitat insularization or that, even if there is a decline, its magnitude and speed are sufficient to warrant conservationists' attention. An assessment must be made anew for each biota, with 2 questions in mind:

1) At the areas we are actually dealing with, what is the approximate rate of any potential species number decline?
2) Is there some "critical area," below which extinction rates are greatly increased and above which they are quite low and not strongly related to area?

Shaffer (1981) has recently summarized evidence for a minimum viable population size. If one assumes a constant average density, this translates into a minimum refuge area. This minimum is determined by a population's need to respond to 4 sorts of random or stochastic events. First is demographic stochasticity—chance aspects of the survival and reproduction of small numbers of individuals. For example, the likelihood that all offspring in some generation will be male is greatly increased in small populations. Second is environmental stochasticity, the usual range of variation in habitat parameters and sizes of interacting species (like predators) that any population faces. Simberloff (1982a) gives examples of how small populations are especially vulnerable to effects of such variation. Third is the occasional occurrence of natural catastrophes like fires and floods, which also wreak greater havoc on smaller populations. Fourth is genetic stochasticity, discussed below, which is more severe the smaller the population.

MacArthur and Wilson (1967) and Richter-Dyn and Goel (1972) provide theoretical models in which extinction from demographic stochasticity is non-linear, with a critical size above which extinction is unlikely. The birth and death rates that are the parameters of these models are unknown for any organism, including prairie plants. There are several reasons for thinking that for plants in general, and many prairie plants in particular, these critical population sizes, if they exist at all, may be very small indeed, and the expected time to extinction usually very long (and, consequently, the rate of species loss very low).

First, many plants are extremely long-lived, either as individuals, such as some trees, or as clones or genets containing many vegetatively produced identical ramets, as in species of *Solidago* and other herbs (and also trees, such as aspen). Harper (1977) observes that a clonally reproducing herb or shrub is genetically equivalent to a large tree lying on its side, and there is evidence for some plants that individual clones may be as old as the most longevous trees. Oinonen (1967a, b, c) has found bracken and ground pine clones of nearly half a mile diameter, weighing many tons, and perhaps 1,500 years old. Similar observations abound for other plants (references in Harberd 1961). Harberd (1961) found in 1 small Scottish population of the fescue *Festuca rubra* very few clones, mostly large and apparently very old. He concludes that this population is not in delicate equilibrium with its environment and is not composed of precarious clones about to be outcompeted by genetically superior ones when such arrive. In fact, new seedlings, even if far superior genetically, would have almost no chance of survival against the well-established, vegetatively maintained existing clones. Mortality of established clones is very low, and any change in genetic composition of the population is exceedingly slow, taking centuries at least. The same conclusions could almost as well be drawn for whether *Festuca* would be replaced by other species, barring major habitat change, and this population comprises an area as small as the smallest of Clinebell's and Glass's prairies.

For *Trifolium repens,* a clover, Harberd (1963) finds more clones and smaller ones, but still fewer clones than ramets, and feels many of these clones are very old. For the grass *Holcus mollis,* there are very few clones in a large population, and each clone seems to span a variety of microhabitats (Harberd 1966). Some are over half a mile across and must be ancient. On the other hand, Harberd and Owen (1968) found in a different population of *Festuca rubra* than the above one that there were many more clones, mostly quite small, while Cahn and Harper (1976) found a similar result in a different population of *Trifolium repens* than that studied by Harberd (1963). It could be that some frequent ecological disturbance, like grazing (Cahn and Harper 1976) or fire (Oinonen 1967a), promotes seedling establishment and thus speeds up the process of genotypic change or species replacement, while in the absence of frequent disturbance such processes are vastly slower than animal ecologists envision.

For prairie plants we know of no data comparable to the above, though many prairie plants are perennial and reproduce vegetatively. Platt (pers. comm.) feels that at least some prairie *Solidago* species consist of very long-lived clones, but many more data are needed. It is likely, however, that at least for prairie perennials any species number decline after insularization will be very slow, at least in the absence of major internal habitat change, unless the islands are minuscule—say, a few square yards. With long-lived plants, a small population is not automatically endangered if its habitat is protected (Rabinowitz 1981). The legendary Ashe's birch (*Betula uber*) apparently persists in a population of only 13 trees and 21 seedlings, and has been as rare as this for nearly a century (Ogle and Mazzeo 1976). If its habitat is protected, there is little reason to think it cannot persist for millennia. Rabinowitz and Rapp (1981) have even shown how certain tallgrass prairie plants that are favored in no habitat and are thus rare wherever found are nonetheless evolutionarily adapted to rarity and are not endangered so long as tallgrass prairie persists in their geographic ranges. On a larger scale, Simpson (1974) suggests that most of the decline in plant species richness in the Galápagos archipelago from the period of maximum Pleistocene areas (peak glaciation) has yet to occur. And Diamond (1972) and Terborgh (1974), for birds, similarly envision the decline as requiring millennia. Again, neither Simpson's study nor those on the avifaunas have direct evidence of how many species were originally present, so there is no proof that a decline occurred.

GENETIC AND OTHER CONSIDERATIONS

Genetic considerations are often said to mandate both very large population sizes and single large refuges rather than several smaller ones of equal total area. Frankel and Soulé (1981) present the most strident exposition of this view. Small populations are a genetic anathema to Frankel and Soule for 2 reasons:

(1) In the short term, inbreeding depression will lead to lower fitness; both survival and reproduction will decrease.

(2) In the long term, the loss of genes resulting from genetic drift will lessen the ability of species to respond evolutionarily to environmental change.

There is no doubt that inbreeding depression is often a very serious matter for small populations of animals, through both the increase in frequency of homozygous recessive major defects and the less obvious but nonetheless real decrease in general fitness that often accompanies the decreasing heterozygosity imposed by inbreeding. Ralls et al. (1979) provide good evidence for the latter effect in several ungulate species, while Brückner (1978) shows inbreeding depression in morphological, physiological, and behavioral traits in honeybees. For plants the evidence is more ambiguous. On the 1 hand, many plants are predominantly selfers, and a study of 4 such species (Brown 1978) shows apparently healthy, persistent populations of each with absolutely no heterozygosity at all. On the other hand, 2 of the species (*Oenothera biennis* and *Avena barbata*) had individual populations that were approximately 50% heterozygous. On average, these 4 species had quite low heterozygosity, and for none of them is there direct evidence that heterozygotes are superior. It appears (e.g., Clegg et al. 1972, Allard 1975, Kahler et al. 1975) that the strongest selective pressure on breeding system in at least 2 of these species is to facilitate preservation of certain multilocus combinations, rather than to optimize degree of heterozygosity per se.

Schaal and Levin (1976) found for the obligately outcrossing perennial prairie herb *Liatris cylindracea* that survivorship, reproductive output, and vegetative production are all greater in more heterozygous individuals, and age of reproductive maturity is lower. Similar results are known for about 10 other plants (reviewed by Schaal and Levin 1976). Of course the fact that genotype *A* will be selected over genotype *B* within a population need not imply that a population of all *A*'s will persist longer than a population of all *B*'s (e.g., Hamilton 1971). This fact plus the existence of homozygous populations blithely persisting apparently indefinitely (previous paragraph) in spite of their genetic homogeneity suggest that inbreeding depression in plants may be less important than the ecological dangers of small population size.

We are skeptical, especially for prairie plants, about the threat that loss of genes by drift in small populations poses to the ability of species to evolve in response to environmental change. Franklin (1980) and Frankel and Soulé (1981) suggest that an effective population size of 500 is required to maintain this ability, while Berry (1971) feels that there is so much genetic variation even in small populations that drift is unlikely to depauperate the gene pool significantly. Further, he notes that, "Observed selection pressures are so strong that any limitations on population size due to a reserve of finite size becoming an ecological isolate, are extremely unlikely to produce random and possibly deleterious genetical changes due to drift."

Whatever the minimum number of individuals a species needs in order to retain sufficient evolutionary potential, whether these should be maintained in 1 large or several smaller sites is, on genetic grounds alone, far from certain. Frankel and Soulé (1981), concerned with the dangers of inbreeding depression, opt for the former arrangement. By contrast, Drury (1974) and Chesser et al. (1980) recommend several small subpopulations. The genetic advantage they see in this strategy is the maintenance of different genes in the different populations, both by chance and by different selective regimes. Inbreeding depression within the subpopulations can be countered by deliberate occasional cross-breeding, but not so much as to obliterate genetic differences between the subpopulations. With prairie plants, for example, one could transplant individuals (or ramets) occasionally or hand-pollinate. The sizes of the subpopulations can, according to Chesser et al. (1980), be very small indeed without major inbreeding depression problems so long as there are occasional migrants. They recommend for 100 deer, for example, starting with 10 refuges of 10 individuals each and maintaining about 20% outbreeding.

Drury (1974), Simberloff and Abele (1976a), Chesser et al. (1980), and others all recognize that the effects of potential catastrophes such as fires, contagious diseases, and storms would be less severe in several small refuges than in 1 large one. Even Frankel and Soulé (1981) concede this point. Drury (1974) and Simberloff (1982b) give examples from the animal literature of the threat to species consisting of 1 population. Surely the same principle applies to plants. Can one doubt that Ashe's birch would be safer were its individuals in 2 widely separated populations of 17 trees each than it is with a single population of 34?

Finally, there may be differences between single large refuges and groups of small ones in management cost and efficacy. Economies of scale would seem to lessen cost for single large refuges (Simberloff and Abele 1982), while Higgs (1981) observes that a single reserve may, on average, reduce detrimental outside influences. For example, control of an entire catchment area makes it easier to control water quality. Similarly, Hirsh (pers. comm.) observes that, if prairies are sufficiently small, their management (e.g., controlled periodic burning) is a nightmare. So at some size, management considerations alone dictate a halt to further subdivision of refuges, just as do biological considerations (see below). On the other hand, there may be increased pressure to "nibble away" at single large reserves just because they are large and so seem able to withstand small inroads of "development" (Higgs 1981). The end of such a process could well be death from a thousand cuts. Helliwell (1976) shows for vascular plants of 106 woods in west Shropshire that small isolated woods are not species-depauperate, and feels that their floras are more "valuable" in a conservation sense (by virtue of the numbers and rarity of their species). He sees the cause for this in the tendency for larger woods to be more intensively managed for timber.

SUGGESTIONS FOR PRAIRIE REFUGES

Two overriding points are clear from our analysis of the prairie plant data and consideration of the genetic, ecological, and conservation literature:

(1) The key requirement for conservation of any prairie plant, or for communities of them, is the establishment of refuges with appropriate habitat.

(2) There is no justification for assuming that single large refuges are automatically the best strategy, though in all circumstances maximum *total* area is probably desirable.

We have throughout said nothing whatever about aesthetic considerations, and do not feel ourselves particularly qualified to do so. It is obvious to us that there is an indescribable aesthetic and even spiritual pleasure that derives from standing in the middle of an enormous prairie such as the Konza, with no intervening habitat breaking the sweep of our vision. No cluster of small prairies will provide this feeling, and for this reason alone it seems imperative to set aside some very large tracts. But we have addressed conservation of biotic diversity, not aesthetic vistas, and it is important to separate these 2 goals. For the first goal alone, enormous refuges need not necessarily constitute the optimal disposition of available money. No amount of ecological research can address the second goal; it is a matter for neurophysiologists and artists.

The above 2 conclusions, however, actually constitute a call for an enormous amount of detailed field research if one is to establish effective refuges. First is all the autecology that goes into finding out exactly what *are* the habitat requirements for the species of interest and the biological idiosyncrasies that make intensive research interesting. Second, even if the above evidence points to several smaller rather than 1 larger refuge as a possible strategy, at some point the individual refuges become so small that extinction rates within them are vastly increased (Simberloff and Abele 1976a), and we want to learn some indication of just what that size is, perhaps by monitoring over time the smallest of Clinebell's and Glass's prairie islands to see how frequent local extinction is. For reasons stated above, such extinction may not be a major problem in any time scale we will worry about for prairie plants even in very small sites, but it would be nice to have data to support this guess. Third, Pickett and Thompson (1978), Foster (1980), L. Gilbert (1980), and Grubb et al. (1982), among others, have all emphasized that many species require various forms of occasional disturbance, such as fire, for their continued existence. Platt (1975) has demonstrated this requirement for a number of prairie plants. Hover and Bragg (1981) note the importance of maintaining a variety of disturbance regimes for conservation of prairie plants, and Opler (1981) reaches similar conclusions for prairie insects. Consequently, whatever arrangement of refuges we settle on, we must ensure that some fraction of them are subjected to the sort of disturbance that will maintain plants of all successional stages. Because prairie succession is relatively rapid, it should be quite feasible to maintain areas at all seral stages simultaneously. Fourth, when species are demonstrated to be so rare that inbreeding depression may rear its ugly head, we should give careful consideration to several emergency measures, such as transplanting and hand-pollination. But such measures ought to be used only *in extremis,* as we know that some completely homozygous plant populations are very viable, rarity *per se* does not mean extinction is imminent, and genetic adaptation to local conditions will be hindered by cross-breeding. Much research is required on all these genetic aspects of prairie plants.

This sounds like a tall order indeed. In a seminal paper on plant communities, Watts (1947) suggested an analogy to T. S. Eliot's admonition to those who would study Shakespeare: "We must know all of it in order to know any of it." Certainly a plant community is a complicated entity, but ecology has come a long way since Watt's pessimistic dictum. In particular, the holistic view of plant communities that so dominated ecology when Watt wrote has been challenged, with the revolution beginning in exactly the same year—1947 (Simberloff 1980). A plethora of population-oriented research has demonstrated that progress in understanding the structure and function of communities is accessible through the analytic approach that has served the chemical and physical sciences so well. We do *not* have to know all about a community to know anything about it, and we are very likely to learn quite a bit about how to conserve communities if we accelerate the sorts of studies outlined above on key species or small groups of species. Throughout, we should beware of the global generality, particularly when it rests on theory or on data from species very different from those that concern us. The small prairie and forest relicts that are apparently suitable for herbs might well lack characteristic mammals, birds, and even insects. Similarly, even if it should turn out that several small prairies typically contain more animal species than single large ones, "small" for animals may be a good bit larger than for plants. Only direct study will address such matters.

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Part 3. Floristics and Biogeography

THE PRAIRIE-FOREST ECOTONE OF THE WESTERN INTERIOR HIGHLANDS: AN INTRODUCTION TO THE TALLGRASS PRAIRIES

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Abstract. The major factors correlated with the distribution of tallgrass prairie include climate, topography, fire, soils, geology, grazing herds, past history, and man. Despite the close proximity of southwestern Missouri, northeastern Oklahoma, northwestern Arkansas, and southeastern Kansas to the historical center for studies in grassland ecology, few studies have examined these factors in this region. Where the western edge of the Interior Highlands lies (along a line from Columbia, Missouri, to Atoka, Oklahoma), there is a transitional boundary between 2 physiognomically distinct vegetation types—tallgrass prairie and deciduous forest. To the west of the Interior Highlands, reconstructed presettlement vegetation maps and early vegetation maps for MO, AR, and OK show predominantly tallgrass prairie with deciduous woodland along rivers. To the east of this line, tallgrass prairie occurred as a mosaic interdigitated with deciduous forest to a distance eastward of about 165 km (100 miles). Paleoecological, archeological, historical, and vegetational information is reviewed for a 650 km × 325 km study area bisected by the western edge of the Interior Highlands, with emphasis on the tallgrass prairies.

INTRODUCTION

The Interior Highlands is a natural physiographic region (Fenneman 1938), composed of the Ouachita and Boston Mountains of northwest Arkansas and eastern Oklahoma and the Springfield and Salem Plateaus of the "Ozarks" of Missouri (Fig. 1, dotted line). To the south and east of the Interior Highlands is the Gulf Coastal Plain; to the north and west is the Central Lowland. The western boundary of the Interior Highlands lies along a line from Columbia, Missouri, to Atoka, Oklahoma. This western boundary roughly coincides with part of the southern margin of the Prairie Peninsula described by Transeau (1935), and there exists here a transitional vegetational boundary between 2 physiognomically distinct vegetation types—tallgrass prairie and deciduous forest.

The major factors that have been correlated with the distribution of tallgrass prairie in North America include climate, topography, fire, soils, geology, grazing herds, past history, and man. In an ecotonal region between 2 physiognomically distinct vegetation types, physical and biotic factors may change, and the vegetation may form a mosaic.

For this survey, I chose a study area 650 km (400 miles) by 325 km (200 miles), bisected by the western edge of the Interior Highlands (Fig. 1, large rectangle). Despite the close proximity of this study area (southwestern Missouri, northwestern Arkansas, northeastern Oklahoma, and southeastern Kansas) to the historical center (Nebraska) for studies in grassland ecology (Tobey 1977), few studies have examined prairie vegetation in this region in conjunction with related environmental factors such as those mentioned above. This paper is an introduction to paleoecology, archeology, and historical descriptions of the study area, as well as a review of the literature on tallgrass prairie vegetation in the prairie-forest ecotone of the western Interior Highlands. Some of the physical and environmental characteristics of the study area are given in Table 1.

PALEOECOLOGY AND ARCHEOLOGY OF THE STUDY AREA

Compared to more northerly regions, the number of paleoecological sites is small, primarily because of a lack of preservation of pollen and plant macrofossils. Some environmental reconstructions (see Fig. 2 for site locations) have been possible for each of the 4 states, but because the time range for each site varies, the chronology of events is poorly known.

In Missouri, caves, rock shelters, and spring sites have shown the best preservation of botanical as well as zoological materials. The best-studied area in Missouri is

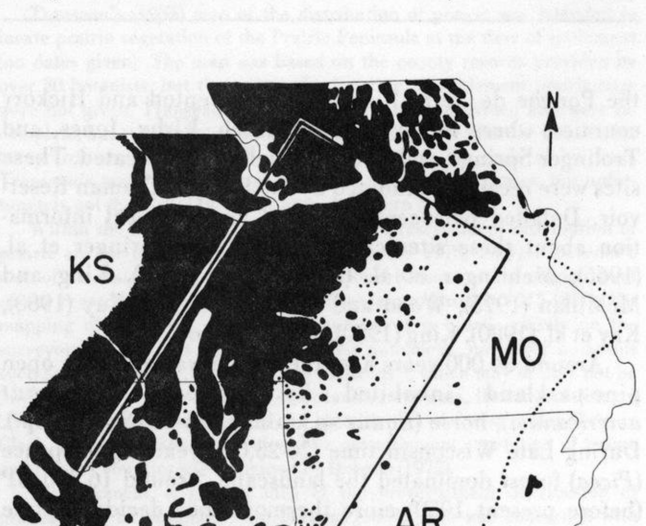

FIG. 1. Approximate distribution of tallgrass prairie (black areas) prior to settlement and major disturbances by white man in Missouri, Arkansas, Kansas, and Oklahoma. Map is based on Sargent (1884) for Arkansas, Duck and Fletcher (1943) for Oklahoma, Küchler (1974) for Kansas, and Schroeder (1981) for Missouri (see text for discussion of sources). Rectangle indicates study area (650 km × 325 km) considered here. Dotted line indicates boundary of the Interior Highlands.

TABLE 1. Selected physical and environmental characteristics of the study area.

1. Longitude: 91-98° West
2. Latitude: 34-40° North
3. Mean annual precipitation: 80-120 cm (32-48 inches) with 100 cm (40 inches) corresponding with the western edge of the Interior Highlands.
4. Mean annual temperature: 14-17° (56-63° F)
5. Mean min. temperature in January: −8 to 0° C (18-32° F)
6. Mean max. temperature in January: 3 to 12° C (38-54° F)
7. Mean min. temperature in July: 18 to 21° C (66-70° F)
8. Mean max. temperature in July: 30 to 34° C (86-94° F)
9. Mean annual radiation: 130-150 kilocalories per cm^2
10. Length of growing season: about 200 days.
11. Elevation: 90-760 m (300-2500 feet). Nearly level to hilly.
12. Geology: Eastern Part—Silurian, Ordovician and Cambrian—igneous (granite) with limestone and dolomite, and sandstone and shale in some places.
    Western Part—Permian, Carboniferous (Permian/Mississippian)—cherty limestone, dolomite.
13. Soils: Utisol—Ozark Highland
    Mollisol—Arkansas River Valley and western part of study area
    Alfisol—along river areas and west of Springfield Plateau
14. *p*H of prairie soil: mostly 5-6 (see Carpenter, Tarr and Rice 1980 for micronutrients also.)
15. Organic matter in prairie soil: 2-3% (see Phillips 1967 for extractable cations and percent base saturation also.)
16. Limit of continental glaciation: To about the Missouri River.
17. Other vegetation types: (a) Oak-Hickory Forest, (b) Floodplain Forest, (c) Pine-Oak Forest, (d) Cedar Forest, (e) Cross Timbers (post oak-blackjack oak forest.)

the Pomme de Terre River valley in Benton and Hickory counties, where Boney, Phillips, Koch, Kirby, Jones, and Trolinger Springs, and Rodgers Shelter were located. These sites were recently inundated by the Harry S Truman Reservoir. Detailed paleoecological and archeological information about these sites can be found in Mehringer et al. (1966), Mehringer et al. (1970), King (1973), King and McMillan (1975), Wood and McMillan (1976), Kay (1980), Kay et al. (1980), King (1980), and Johnson (1980).

Around 34,000 years ago, the region was probably open pine-parkland inhabited by mastodon (*Mammut americanum*), horse (*Equus* sp.), and musk-ox (*Symbos* sp.). During Late Wisconsin time (20-25,000 years ago), spruce (*Picea*) forest dominated the landscape. Around 16,500 BP (before present 1950) more thermophilous deciduous tree species, such as ash (*Fraxinus*), oak (*Quercus*), and willow (*Salix*), were present along with the spruce. Spruce forest began to disappear around 13,500 years ago. The last 6000 years of the spring deposits represent oak-hickory (*Quercus-Carya*) forest.

There are no known sites in Kansas within the study area, although Muscotah Marsh and Arrington Marsh are close (Gruger 1973). Muscotah Marsh has a complete record of vegetation from 11,300 BP to the present. The greatest occurrence of prairie is indicated by pollen of *Ambrosia, Amorpha* and *Petalostemum* 9,000 to 5,000 years BP, which correlates with the warm and/or dry period known as the Hypsithermal.

Environmental and vegetational reconstructions for eastern Oklahoma are found in Vehed by pollen of *Ambrosia, Amorpha* and *Petalostemum* 9,000 to 5,000 years BP, which correlates with the warm and/or dry period known as the Hypsithermal.

Environmental and vegetational reconstructions for eastern Oklahoma are found in Veh believed to represent the regional oak-savanna vegetation at the end of the Hypsithermal Period.

Moister and/or cooler conditions then followed, producing an oak-history forest, which dominated until about 2700 years BP. Around 1700 years BP, pine (*Pinus*) forest began to increase within the oak-history forest, and the forest canopy probably closed. A drier period similar to that in northeastern Oklahoma (Hall 1982) is seen around 1000-500 years ago. About 250 years ago, wetter conditions returned, which Albert (1981) correlated with the Little Ice Age of the 17th and 18th centuries.

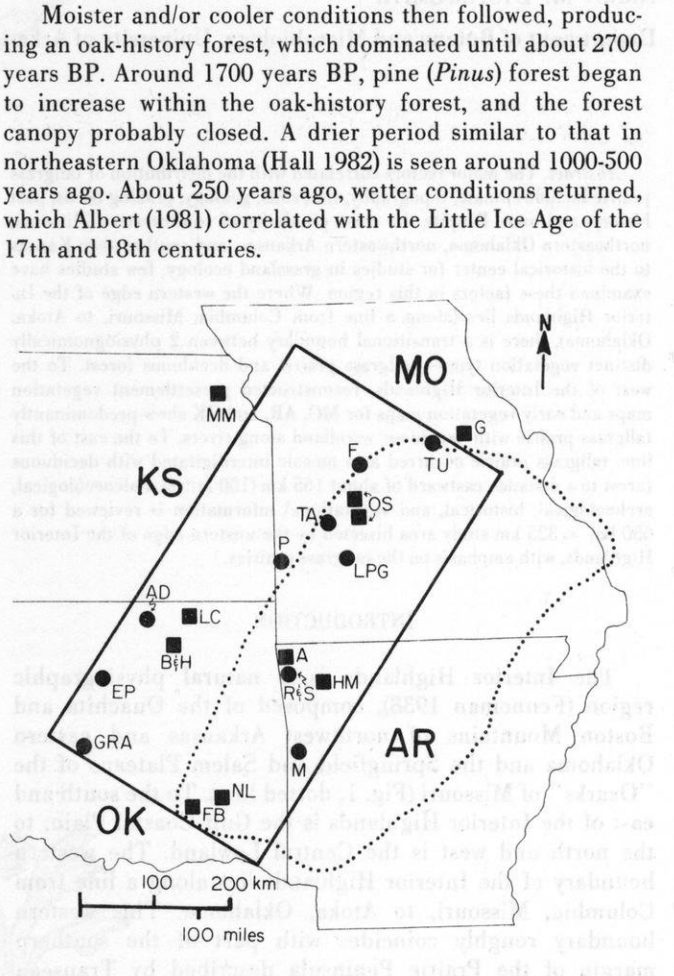

FIG. 2. Squares denote location of paleoecological and archeological sites mentioned in the text. Dots denote existing prairies for which publications are listed in Table 2.

KEY TO SYMBOLS

Paleoecological/archeological sites		Prairie sites	
A	Albertson site	AD	Adams Ranch, IBP OSAGE site
B&H	Birch and Hominy Creeks	EP	Ecology Preserve, OK. State Univ.
FB	Ferndale Bog		
G	Graham Cave	F	Friendly Prairie
G	Graham Cave	GRA	Grassland Research Area, Univ. OK
HM	Huntsville Mounds		
LC	Little Caney River	LPG	La Petite Gemme Prairie
MM	Muscotah and Arrington Marshes	M	Massard Prairie
		P	Prairie State Park
NL	Natural Lake	R&S	Rice and Stump Prairies
OS	Ozark Springs (Boney, Phillips, Jones, Koch, Kirby, and Trolinger), and Rodgers Shelter in the Pomme de Terre River Valley.	TA	Taberville Prairie
		TU	Tucker Prairie

Hall (1982) summarizes the Late Holocene paleoecology of northeastern Oklahoma. The analyses are based on pollen and land snails from rock shelters in the Osage Hills within Cross Timbers vegetation of post-oak (*Quercus stellata*) and black-jack oak (*Q. marilandica*), but close to tallgrass prairie. Fossils from sites along Birch Creek, Hominy Creek, and Little Caney River represent the last 2000 years. From 2000 to 1000 years BP the climate was apparently much moister in this region than it is today, based on (1) higher frequencies than present of hickory (*Carya*) pollen recorded in upland sites, (2) higher frequencies of grass (Poaceae) pollen recorded in lowland sites, indicating a high water table, and (3) abundance of the striped forest snail (*Anguispira alternata*), a floodplain and mesic forest species. Other pollen profiles in northeastern Oklahoma are undated (Vehik and Pailes 1979).

Early studies within Arkansas recognized Ozark Bluff Dweller sites containing native as well as cultivated plant material (Gilmore 1931, Harrington 1960). More recently studied sites, such as the Albertson rock shelter and Huntsville mounds, provide little environmental interpretations for 1100 to 500 radiocarbon years BP (Sabo 1982), because little uncarbonized organic matter or pollen is preserved.

For a broad discussion of vegetational change within the Prairie Peninsula see Wright (1968). Cole (1971) also has a general correlative discussion of post-glacial times within the Ozark Highlands. Discussions of archeology and human ecology can be found in Chapman (1975), Wendland (1978), and Henry et al. (1979).

Some additional environmental information may be available from the study of pimple or prairie mounds, which are common in the study area, especially in Arkansas and Oklahoma (Arnold 1960, Cain 1974). Although no hypothesis of formation has been proved, these mounds may have been formed under depositional and/or erosional conditions of wetter or drier climates in the past. Additionally tree-ring analysis of red cedar (*Juniperus virginiana*) has shown the potential for climatic reconstruction in Missouri for the last 500 years (Guyette et al. 1980). The earlier tree-ring work of Harper (1961) in Oklahoma with post-oak (*Q. stellata*) indicates 55 drought years in the past 250 years.

Some information on modern pollen rain would be useful for interpreting paleoecological data. Within the study area, only 3 persons have examined modern pollen samples in moss polsters and ponds (King 1973, Peterson 1978, Key 1981). All of these were in relation to contiguous forest, however, and not prairie.

HISTORICAL DESCRIPTIONS

Numerous explorers, traders, naturalists, and settlers traveled through the Ozark region and adjacent areas, particularly along the waterways. Lewis and Clark explored the Missouri River and described some of the vegetation as they headed west (Thwaites 1904-5). Some of the best landscape and vegetational notes for the area in question were made by Henry Schoolcraft and Thomas Nuttall. Schoolcraft explored the Ozark region in 1818 and 1819, and many of his writings were published, such as his *Journal of a Tour* (Schoolcraft 1821). Thomas Nuttall traveled through the Ozarks of Arkansas and parts of southeastern Oklahoma in 1819. He noted that as he approached the region of the present AR-OK stateline, the prairies became more prevalent (Nuttall 1905). Other important expeditions where vegetation was recorded were by Washington Irving in northeastern Oklahoma in 1832 (Thwaites 1904-7), and by the Dragoon Expedition of 1834, which included the well-known painter of Indian life, George Catlin (Morris et al. 1976).

In 1821, Jacob Fowler traveled through eastern Oklahoma and recorded in his journal numerous prairies and buffalo sightings (Coues 1898, Fessler 1930). In 1834 Featherstonhaugh traveled through the region between the Missouri and Red Rivers, describing the geology and making mention of the mixture of forest and prairie within the region (Featherstonhaugh 1835). Northwestern Arkansas was described by Leo Lesquereux (1860), a botanist working with Daniel Dale Owen on a geological survey. Further vegetational and historical information may be found in Branner and Coville (1891), Morris et al. (1976) and Rafferty (1982). Some excerpted historical accounts of both prairie and timber have been included in Beilman and Brenner (1951), Ray and Lawson (1953), Steyermark (1959), and Christisen (1967).

PRESETTLEMENT DISTRIBUTION OF PRAIRIE

The approximate presettlement distribution of tallgrass prairie in the study area is shown in Fig. 1. It is based on different sources for each state, as discussed below.

Transeau's (1935) map of the distribution of prairie was intended to locate prairie vegetation of the Prairie Peninsula at the time of settlement (no dates given). The map was based on the county records provided by over 30 botanists, but the criteria for locating presettlement prairie sites were not given. Transeau admitted that the maps provided him were incomplete, but stated that additional records would not alter the boundaries for prairie vegetation, which is probably true at the scale of his map. Transeau's map includes Missouri and northwestern Arkansas, but unfortunately not the rest of the study area of concern here.

Within the study area, the best data for presettlement distribution of prairie are for the state of Missouri (Schroeder 1978, 1981). Schroeder's map of the distribution of prairie in Missouri is based on the original land survey records of the General Land Office (approximately 1815-1850). His mapping of prairie is conservative because it is based entirely on the surveyors' mention of "prairie" in their notebooks, not other notations such as "long grass", "glade", and "barrens", which may or may not be interpreted as prairie. From the same land survey data, Howell and Kucera (1956) have published maps of the distribution of forest and prairie in Clark, Dade, and Boone counties. The presettlement vegetation of Saline and Cooper counties was examined by Hobson (1972).

For Arkansas, a general idea of the presettlement distribution of prairie must be obtained from Sargent (1884), who was concerned with forest trees and their economic importance. For the area of Arkansas within the study area, I know of only 1 reconstruction of vegetation from land survey records. Miller (1972) delimited upland and lowland prairie, oak barrens, and upland and lowland forest for Benton and Washington counties in the northwesternmost corner of the state. Unfortunately he did not state his criteria for distinguishing these 5 vegetation groups from the information in the land survey records. Most of his upland prairies do coincide with the dark-surface soils of presumed prairie origin mapped by Phillips (1967).

Maps of presettlement vegetation based on land survey data are badly needed but unavailable for Oklahoma and Kansas. There is apparently only one published vegetation map for Oklahoma (Duck and Fletcher 1943). It was compiled for wildlife purposes, and the source of its data is unstated. Similarly for Kansas, there is no map available that reconstructs presettlement vegetation. Küchler's (1974) potential vegetation map for Kansas, as the only available source, was used here.

TABLE 2. Prairie vegetation studies within the study area. Reference lists are not necessarily complete. Locations are shown on Fig. 2.

PRAIRIE SITES	LOCATIONS	REFERENCES	TOPICS
Arkansas			
Massard Prairie	Sebastian Co.	Armstrong 1941	Floristics, phenology
		Armstrong and Moore 1957	Floristics, phenology
Rice & Stump Prairies	Benton Co.	Clark 1977	Floristics
Missouri			
Friendly Prairie	Pettis Co.	Hurd and Christisen 1975	Floristics, phenology & productivity
La Petite Gemme Prairie	Polk Co.	Timme 1982, 1983	Bryophyte communities
Prairie State Park	Barton Co.	park brochure	Floristics
Taberville Prairie	St. Clair Co.	Brown 1962	Floristics
		Toney [no date]	Floristics
		Christisen 1981	Vegetation importance to greater prairie chicken
Tucker Prairie	Callaway Co.	Drew 1947, Kucera 1956	Effects of grazing on plant composition
		Kucera 1960	Forest encroachment
		Brown 1962	Floristics
		Kucera and Ehrenreich 1962	Effects of annual burning
		Koelling and Kucera 1965	Productivity, mineral cycling
		Dahlman and Kucera 1965	Below-ground productivity
		Kucera, Dahlman and Koelling 1967	Productivity
		Kirkham 1970, Kucera and Kirkham 1971	Litter effects on soil respiration
		Zimmerman 1971, Zimmerman and Kucera 1977	Productivity of *Solidago* versus grasses
		Rabinowitz et. al. 1979	Biomass, neighborhood structure
		Rabinowitz and Rapp 1980	Seed rain
		Rabinowitz 1981	Buried viable seeds
		Rabinowitz and Rapp 1981	Grass dispersal
		Rabinowitz et al. 1981	Phenology versus pollination mode
		Callahan and Kucera 1981	Magnesium flux and storage
Oklahoma			
Adams Ranch IBP OSAGE site	Osage Co.	Conant and Risser 1974	Height, basal cover, leaf area, above-ground biomass
		Risser 1976	Above- and below-ground biomass, energy flow
		Sims et al. 1978	Shoot and root biomass
		Sims and Singh 1978a, 1978b	Biomass, turnover, energy flow
		Parton and Risser 1980	Impact of management
		see Milby (1977) and Risser et al. (1981) for others	
Ecology Preserve, Oklahoma State Univ.	Payne Co.	Mueller 1964	Phenology
		Petranka and McPherson 1979	Invasion by *Rhus*
		Tarr et al. 1980	Percent composition and species diversity
Grassland Research Area, Univ. of Oklahoma	McClain Co.	Kelting 1954	Grazing effects on composition and productivity
		Ahshapanek 1959, 1962	Phenology
		Rice et al. 1960	Grass dispersal, minerals
		Hamp et al. 1972	Fungi
		Rice and Parenti 1978	Causes of decreased productivuty
		Tarr et al. 1980	Percent composition and species diversity
		Collins and Adams 1983	Succession

EXISTING PRAIRIE SITES

Missouri has the most active preservation program of any state within the study area (Christisen 1973). Locations of prairie preserves owned by the Missouri Prairie Foundation, The Nature Conservancy, and the Missouri Departments of Natural Resources and of Conservation can be found in *Public Prairies of Missouri* (Toney 1981). There are now 35 preserves, most within the study area.

For some high quality areas of tallgrass prairie within the Interior Highlands, Zachry and Dale (1979) should be consulted. Most of the prairie areas remaining in Oklahoma and Kansas are privately owned and used as hay meadows, which are mowed once or twice annually. Crow (1974) and Ruby (1953) describe some prairie remnants in northwestern Arkansas. All current Arkansas prairie preserves are outside the study area. The respective Heritage Programs for the various states also maintain files on remnant prairie sites.

VEGETATIONAL STUDIES OF MODERN TALLGRASS PRAIRIE

Literature on prairies and other vegetation in Oklahoma can be found in Kelting and Penfound (1953), Milby and Penfound (1964), and Milby (1977). Literature on prairies and other vegetation in Arkansas can be found in Dale (1963) and Pell (1980).

Taxonomic references for the study area are Steyermark (1963) and Kucera (1961) for Missouri, Waterfall (1972) for Oklahoma, Smith (1978) for Arkansas, and Bare (1979) and Owensby (1980) for Kansas. Barkley (1977) is helpful for distributions of species although it is very weak for Arkansas records. A few theses contain floras for certain prairies (Brown 1962), or for certain counties, such as McDonald (1974, 1976) for Washington Co., OK, or Barber (1980) for Franklin Co., AR.

General descriptions of the vegetation within the study area may be found in Bruner (1931), Blair (1938), Blair and Hubbell (1938), Crow (1974), Küchler (1974), and Thom and Wilson (1980). Bare and McGregor (1970) discuss the phytogeography of Kansas, including the association of floristic groups with prairie habitats.

A few prairie sites within the study area have been studied in detail. Their locations are shown in Fig. 2, and associated references are listed in Table 2. These studies provide some information on species composition, productivity, energy and mineral cycling, phenology, seed bank and seed rain data, and the effects of management of tallgrass prairies. The more intensely studied sites are those near universities and owned or managed by them. Estes and Tyrl (1976) should be consulted for a variety of related studies on grasses and grasslands in Oklahoma.

The greatest variety of studies on any 1 site has been on the Adams Ranch in Osage Co., OK (Fig. 2). This ranch served as the International Biological Program's (IBP) tallgrass prairie ecosystem. Risser et al. (1981) is based on the 3-year study at the IBP site as well as on older data from Weaver and others on the tallgrass prairie ecosystem in general. The book does not pertain strictly to southern tallgrass prairies, but includes considerable northern United States data as well. The book should be consulted for information on geology, climate, flora, primary production, invertebrates, avifauna, small mammals, grazing, nutrients, water, fire, and pesticides.

There are apparently very few regional studies, and I know of only 3. An analysis of 15 tallgrass prairies throughout Oklahoma (Tarr et al. 1980) indicates that little bluestem (*Andropogon scoparius* = *Schizachyrium scoparium*) is the most important prairie species and that its percent of the prairie composition is inversely related to precipitation. Eight of the 15 sites occur within the study area. The data for these sites indicate that little bluestem, big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), broom sedge (*Andropogon virginicus*), and sedges (*Cyperaceae*) are the dominant species on the basis of % composition. Species diversity and basal cover do not change across Oklahoma.

The other 2 studies are in northeastern Oklahoma, northeast of Tulsa. Buck (1959) and Buck and Kelting (1962) report the September and October species composition of 68 tallgrass prairie sites. Ray (1957, 1959) examined the percent areal cover and frequency of plant species occurring in 3 prairies in late July in Rogers County, Oklahoma.

No published vegetational studies are known for the southeastern part of Kansas within the study area.

RESEARCH NEEDED

This introduction to the prairie vegetation in the vicinity of the Interior Highlands makes it apparent that although we have somewhat detailed information from a number of prairie sites, we do not have a unified picture of the entire region. More quantitative vegetational and environmental data are needed for a complete understanding of the dynamics of tallgrass prairie along the southern edge of the Prairie Peninsula. On a regional scale, what are the most likely controlling parameters of the distribution of tallgrass prairie? Is topography of primary importance here because of its relatedness to fire movements, climate, geology, and soils? How do biotic and abiotic parameters change across the ecotone?

Additional studies about the full-, late-, and post-glacial environmental conditions of the region, with complete and dated sequences, should answer the following questions: (1) What was the extent of prairie distribution in full-glacial times? (2) Is prairie, as we know it today, only a recent assemblage of plant species, or have these species existed together for thousands of years? (3) In post-glacial times, did prairie migrate eastward during the Hypsithermal on the southern edge of the Prairie Peninsula, as it apparently did in the north? (4) If prairie vegetation did migrate eastward during the Hypsithermal, did it do so into the Interior Highlands, or did the hilly topography and numerous rivers and streams serve as fire breaks? Also needed are pollen analog data from prairie vegetation existing now, so that future interpretations of pollen diagrams from prairie regions can be more accurate. Additionally, what was the presettlement distribution of prairie in Arkansas, Oklahoma, and Kansas?

Studies on the ecosystem and community level should be extended beyond the 1 IBP site. What are the effects of various management practices on species diversity, and above- and below-ground productivity, and on competitive abilities of plants? Are these effects consistent over the entire region? What are the long-term effects?

At the community level, do the prairies with greater species diversity have more total basal cover, presumably because of species packing into available niches? Also, how does species diversity change across the ecotone? What are the species associations with regional environmental parameters and management practices? How long does it take for tallgrass prairie to reach a late successional stage?

Some questions at the population level that could be examined are (1) What are the life-history traits of prairie plants that allow them to survive under drought conditions, yet remain competitive in more humid conditions? (2) How do prairie plants compete with woody shrubs and trees? (3) How do perennial prairie species become established in

prairie where competition for light and nutrients must be intense?

Data that answer some of these questions should help with the preservation and re-establishment of tallgrass prairie. A specific question of interest is, What is the appropriate size of prairie preserves for maximum protection of its gene pools?

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THE WAH-SHA-SHE PRAIRIE NEAR ASBURY, JASPER COUNTY, MISSOURI

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Abstract. Periodic collections of vascular flora were made from October 1980 through June 1982 on the Wah-Sha-She Prairie, 3.2 km north of Asbury, Jasper County, Missouri. This tract (acquired in 1975) of 64.75 ha is a part of the preserved prairie system administered by the Missouri Department of Conservation. The prairie has a history of being used as a hay meadow. Present management includes mowing for hay or burning.

The upland prairie is dominated by big bluestem (*Andropogon gerardii*), little bluestem (*A. scoparius*), and Indian grass (*Sorghastrum nutans*). In addition to the 3 grasses, the swales are occupied by various sedges. An impoundment of approximately 5 ha occupies the major portion of a large draw that traverses the prairie from west to east. This impoundment has created a complex of aquatic and wetland communities.

The plant check-list includes 269 taxa comprising 61 families: 65% (175) are forbs, 27% (73) are grasses, sedges, or rushes, and 8% (21) are woody. Perennials dominate the prairie. Thirteen of the taxa were determined to be of non-North American origin.

INTRODUCTION

For the past several years, the Missouri Department of Conservation, aided by The Nature Conservancy and other interested groups, has acquired several prairie remnants in the tall grass prairie region of Missouri (Anon. 1978). These prairies are under a management plan of rotational mowing and/or burning and are open to the public for viewing and study. The Friendly Prairie near Sedalia has been studied extensively (Hurd and Christisen 1975; Hurd 1982), whereas others are in various stages of study. Unpublished check-lists of the vascular plants are available for Prairie State Park near Liberal (Barton County) and for Taberville Prairie (St. Clair County). The Wah-Sha-She Prairie was chosen for an intensive floristic study as a contribution to the overall investigation of the public prairies of Missouri. The study was begun in October 1980 and continued through June 1982. Weekly or bi-weekly visits were made to the prairie during the growing seasons. Prior to this study, a preliminary check-list had been prepared by Thomas E. Toney, Prairie Biologist, Missouri Department of Conservation (personal communication 1980).

STUDY AREA

The Wah-Sha-She Prairie is a 64.75 ha remnant of upland tall grass prairie located in SE ¼ Sec. 31, T30N, R33W (37° 15′ N. Lat.; 94° 32′ W. Long.) approximately 3.2 km north of Asbury, Jasper County, Missouri (Fig. 1). The prairie is a unit of the Kathryn Ordway Prairie System and was purchased in 1973 with funds from The Nature Conservancy. Since 1975 it has been managed by the Missouri Department of Conservation. Prior to 1973, the area was mowed for hay annually but from 1973 to 1975 only alternate halves of the area were cut. For the following 5 years, the entire area was unmowed due to wild fires (Toney 1980, personal communication). In July 1981, the south portion was mowed for hay, while the north portion was burned in spring 1982.

The prairie is relatively flat; most of the area occurs within a range of elevation from 274 to 277 m. A large draw traverses the tract with drainage generally oriented from west to east. A dam (of unknown age) provides an

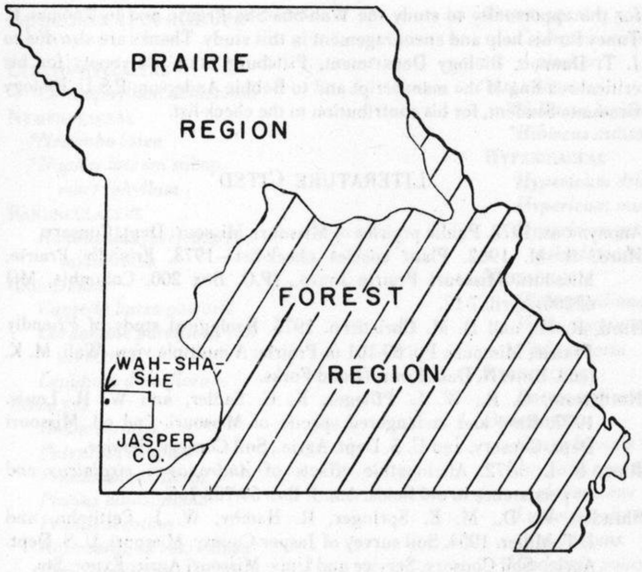

FIG. 1. Wah-Sha-She Prairie location in Missouri prairie region.

impoundment that, at high water levels, extends to the west boundary of the prairie (Fig. 2).

The soils are acidic prairie claypan soils, grayish brown to dark-gray silt loams derived from Pennsylvanian non-calcareous sandstones and shales. The draws, or breaks, are a complex of alluvial soils (Shrader et al. 1954).

The climate of Wah-Sha-She Prairie is continental, with hot summers and frequent summer droughts. Climatic data (summarized for a 10-year period, 1972-1981) from Pittsburg State University Weather Station, approximately 15.5 km northwest of the study area, revealed a mean annual temperature of 21.4°C. Mean monthly temperatures varied from 0.4°C in January to 28.6°C in July. The frost-free season varied from 194 to 237 days with a mean of 219 days. Annual precipitation during this period ranged from 59.7 to 149.9 cm, with a mean of 108.9 cm. Approximately ¾ of the precipitation recorded occurred during the growing season.

Andropogon gerardii[1] and *A. scoparius* are the predominant grasses on the prairie south of the impounded draw; these 2 grasses, along with *Sorghastrum nutans* also predominate in the portion of the prairie north of the draw. A complex of aquatic and wetland communities under the influence of the impoundment (including those below the dam) are evident.

RESULTS

Two hundred and sixty-nine plant taxa distributed in 61 families, 167 genera, 265 species, 2 subspecies, and 46 varieties were collected during the study (Appendix 1). The families are arranged according to Steyermark (1963) with genera, species, and varieties arranged alphabetically under each family. Varietal epithets are not listed when only the typical variety was collected. Voucher specimens are on file in the Theodore M. Sperry Herbarium (KSP) of Pittsburg State University.

Of the taxa present in the study area, 175 were forbs, 73 were grasses, sedges, or rushes, and 21 were woody species. A predominant 187 (70%) taxa were perennial including 77% of the grasses, sedges, and rushes, and 63% of the forbs. Only 13 taxa were introduced from other continents (7 forbs, 5 grasses, and 1 woody species); of these 8 were annuals or biennials. In addition, Kentucky bluegrass (*Poa pratensis*) is undoubtedly adventive to this area from the eastern United States.

Approximately one-half of the taxa from the study area are members of the following 4 families: Compositae (47); Gramineae (46); Cyperaceae (21); Leguminosae (21). Thirty (49%) of the plant families were represented by only 1 species, while 9 (15%) had only 2 species.

DISCUSSION

It is difficult to assess the effects of the impoundment on the flora of the Wah-Sha-She Prairie. Prior to the impoundment, the large draw traversing the prairie was undoubtedly effective in maintaining drainage without creating areas of long-standing water. However, the lower areas in the drainage pattern would have supported various aquatic or semi-aquatic grasses, sedges, rushes, and certain forb species. It is estimated that 29 taxa present were there as a direct result of the impoundment. These include all of the aquatic species as well as those species commonly found around impoundments in the prairies in this area. These taxa have been indicated with asterisks in Appendix 1.

Some plants are of particular interest in this study. *Aster paludosus* subsp. *hemisphericus* is listed as rare in Missouri (Nordstrom et al. 1977). Nordstrom et al. define a rare species or subspecies as "one that is present in Missouri in small numbers." They also state that such species may be present in substantial numbers in other parts of its range. Hundreds of these asters were observed growing on the Wah-Sha-She during the late summer and autumn of 1981. *Desmanthus illinoensis* was represented by only 1 small clump in the prairie but it was plentiful along unmowed, unburned, road-side ditches. Evidently this species is not tolerant of mowing and/or burning. *Dodecatheon meadia, Castilleja coccinea,* and *Sabatia campestris* are either very low in number or absent on the prairie if the area has not been mowed or burned recently. These 3 species were not found in the spring of 1981 although they are usually present. It is suggested that the build-up of dead plant material

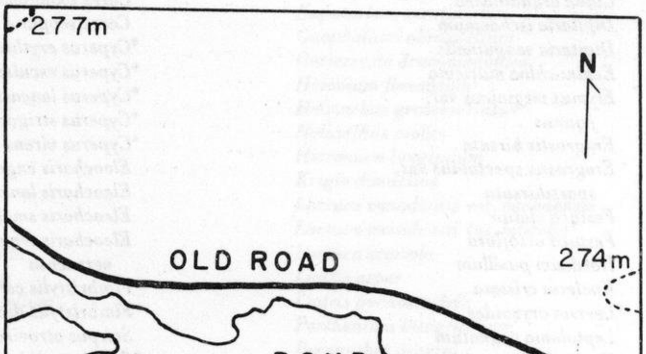

FIG. 2. Major physical features of Wah-Sha-She Prairie.

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[1] Nomenclature follows Steyermark (1963).

precludes or inhibits their germination.

Also of interest is the relationship of an old road along the north side of the draw (Fig. 2) to the presence of certain plant species. The age of the road is unknown, but it has been used in recent years. The road is quite evident on 1938 aerial photographs of the area. The major species growing in the abandoned road is broom sedge (*Andropogon virginicus*), which is associated with such forbs as fireweed (*Erechtites hieracifolia*) and various species of *Lespedeza* and *Gerardia.* Rice (1972) reported that broom sedge directly inhibits growth of little bluestem and other species that would normally replace it in later successional stages; thus, it appears that broom sedge will persist for many more years even under proper management.

Continued collections and study will be necessary on the Wah-Sha-She Prairie before a complete species list is finally compiled.

ACKNOWLEDGMENTS

Appreciation is expressed to the Missouri Department of Conservation for the opportunity to study the Wah-Sha-She Prairie and to Thomas E. Toney for his help and encouragement in this study. Thanks are also due to J. T. Dawson, Biology Department, Pittsburg State University for his critical reading of the manuscript and to Bobbie Anderson, P.S.U. Biology Graduate Student, for his contribution to the check-list.

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APPENDIX 1. VASCULAR PLANTS OF THE WAH-SHA-SHE PRAIRIE.

TYPHACEAE
**Typha latifolia*
NAJADACEAE
**Potamogeton diversifolius*
ALISMATACEAE
**Sagittaria latifolia*
GRAMINEAE
Agrostis hyemalis
Agrostis perennans
Alopecurus carolinianus
Andropogon gerardii
Andropogon scoparius
Andropogon virginicus
Aristida longispica
Aristida oligantha
Aristida purpurascens
Aristida ramosissima
Bromus racemosus
**Cinna arundinacea*
Digitaria ischaemum
Digitaria sanguinalis
Echinochloa muricata
Elymus virginicus var. *jejunus*
Eragrostis hirsuta
Eragrostis spectabilis var. *sparsihirsuta*
Festuca elatior
Festuca octoflora
Hordeum pusillum
Koeleria cristata
**Leersia oryzoides*
Leptoloma cognatum
Panicum agrostoides
Panicum capillare
Panicum flexile
Panicum lanuginosum var. *fasciculatum*
Panicum lanuginosum var. *lindheimeri*
Panicum oligosanthes var. *helleri*
Panicum scoparium
Panicum virgatum
Paspalum ciliatifolium var. *muhlenbergii*
Paspalum floridanum
Paspalum laeve var. *circulare*
Paspalum pubiflorum var. *glabrum*
Phalaris caroliniana
Phleum pratense
Poa pratensis
Setaria geniculata
Setaria glauca
Sorghastrum nutans
Spartina pectinata
Sphenopholis obtusata
Tridens strictus
Uniola latifolia
CYPERACEAE
Carex bicknellii
Carex brevior
Carex bushii
Carex lupulina
Carex meadii
Carex oklahomensis
Carex scoparia
**Cyperus erythrorhizos*
**Cyperus esculentus*
**Cyperus lancastriensis*
**Cyperus strigosus*
**Cyperus virens*
Eleocharis engelmannii
Eleocharis lanceolata
Eleocharis smallii
Eleocharis tenuis var. *verrucosa*
Fimbristylis caroliniana
Fimbristylis dichotoma
Scirpus atrovirens
**Scirpus validus* var. *creber*
Scleria triglomerata
COMMELINACEAE
Tradescantia ohiensis
JUNCACEAE
Juncus acuminatus
Juncus biflorus
Juncus brachycarpus
Juncus effusus var. *solutus*
Juncus interior
Juncus torreyi
LILIACEAE
Allium canadense
Camassia scilloides
Erythronium albidum var. *mesochoreum*
Nothoscordum bivalve
AMARYLLIDACEAE
Hypoxis hirsuta
IRIDACEAE
Sisyrinchium campestre
ORCHIDACEAE
Spiranthes cernua
SALICACEAE
**Populus deltoides*
**Salix nigra*
ULMACEAE
Celtis occidentalis
Ulmus americana
Ulmus rubra
MORACEAE
Morus rubra
URTICACEAE
Boehmeria cylindrica
Parietaria pensylvanica
POLYGONACEAE
**Polygonum coccineum*
**Polygonum hydropiperoides* var. *hydropiperoides*
**Polygonum hydropiperoides* var. *opelousanum*
**Polygonum lapathifolium*
**Polygonum pensylvanicum* var. *laevigatum*
**Polygonum punctatum*
Rumex altissimus
Rumex crispus
CHENOPODIACEAE
Chenopodium album
AMARANTHACEAE
Amaranthus tamariscinus
PHYTOLACCACEAE
Phytolacca americana
PORTULACACEAE
Claytonia virginica
CARYOPHYLLACEAE
Cerastium brachypodum

*Plant presence due to the impoundment.

Appendix 1, continued

- CERATOPHYLLACEAE
  - *Ceratophyllum demersum
- NYMPHAEACEAE
  - *Nelumbo lutea
  - *Nuphar luteum subsp. macrophyllum
- RANUNCULACEAE
  - Ranunculus fascicularis var. apricus
- CRUCIFERAE
  - Capsella bursa-pastoris
  - Cardamine parviflora var. arenicola
  - Lepidium densiflorum
- ROSACEAE
  - Geum vernum
  - Potentilla simplex
  - Prunus angustifolia
  - Prunus munsoniana
  - Prunus serotina
  - Rosa carolina var. villosa
  - Rosa multiflora
  - Rubus flagellaris
- LEGUMINOSAE
  - Amorpha canescens
  - Amorpha fruticosa
  - Astragalus mexicanus var. trichocalyx
  - Baptisia leucantha
  - Baptisia leucophaea
  - Cassia fasciculata
  - Crotalaria sagittalis
  - Desmanthus illinoensis
  - Desmodium paniculatum var. dillenii
  - Desmodium sessilifolium
  - Lespedeza capitata
  - Lespedeza striata
  - Lespedeza virginica
  - Melilotus alba
  - Petalostemum candidum
  - Petalostemum purpureum
  - Psoralea psoralioides var. eglandulosa
  - Psoralea tenuiflora
  - Schrankia uncinata
  - Strophostyles leiosperma
  - Stylosanthes biflora
- LINACEAE
  - Linum medium var. texanum
  - Linum sulcatum
- OXALIDACEAE
  - Oxalis dillenii
  - Oxalis violacea
- GERANIACEAE
  - Geranium carolinianum
- POLYGALACEAE
  - Polygala incarnata
  - Polygala sanguinea
  - Polygala verticillata var. ambigua
- EUPHORBIACEAE
  - Acalphya virginica
  - Croton capitatus
  - Crotonopsis elliptica
  - Euphorbia corollata
- CALLITRICHACEAE
  - *Callitriche heterophylla
- ANACARDIACEAE
  - Rhus copallina var. latifolia
  - Rhus glabra
  - Rhus radicans var. vulgaris
- RHAMNACEAE
  - Ceanothus americanus var. pitcheri
- MALVACEAE
  - *Hibiscus lasiocarpus
  - *Hibiscus militaris
- HYPERICACEAE
  - Hypericum drummondii
  - Hypericum mutilum
  - Hypericum punctatum var. pseudomaculatum
- VIOLACEAE
  - Viola papilionacea
  - Viola sagittata
  - Viola sororia
- LYTHRACEAE
  - Rotala ramosior var. interior
- ONAGRACEAE
  - Gaura biennis var. pitcheri
  - *Jussiaea repens var. glabrescens
  - Ludwigia alternifolia var. pubescens
  - *Ludwigia palustris var. americana
  - Oenothera biennis var. canescens
  - Oenothera linifolia
- HALORAGACEAE
  - *Myriophyllum heterophyllum
- UMBELLIFERAE
  - Eryngium yuccifolium
  - Polytaenia nuttallii
  - Ptilimnium nuttallii
- CORNACEAE
  - Cornus racemosa
- PRIMULACEAE
  - Centunculus minimus
  - Dodecatheon meadia
- EBENACEAE
  - Diospyros virginiana
- GENTIANACEAE
  - Gentiana puberula
  - Sabatia campestris
- APOCYNACEAE
  - Apocynum cannabinum
- ASCLEPIADACEAE
  - Asclepias hirtella
  - Asclepias incarnata
  - Asclepias stenophylla
  - Asclepias tuberosa
  - Asclepias viridis
- BORAGINACEAE
  - Lithospermum arvense
- VERBENACEAE
  - Verbena hastata
- LABIATAE
  - Lycopus americanus
  - Lycopus rubellus
  - Physostegia angustifolia
  - Physostegia virginiana
  - Pycnanthemum tenuifolium
  - Salvia azurea var. grandiflora
  - Scutellaria parvula
- SOLANACEAE
  - Physalis heterophylla
  - Physalis pubescens
  - Solanum carolinense
- SCROPHULARIACEAE
  - Buchnera americana
  - Castilleja coccinea
  - Gerardia fasciculata
  - Gerardia skinneriana
  - Gerardia viridis
  - Linaria canadensis var. texana
  - Lindernia anagallidea
  - Penstemon arkansanus
  - Penstemon tubaeflorus
- LENTIBULARIACEAE
  - *Utricularia gibba
- ACANTHACEAE
  - Ruellia humilis var. longiflora
- PLANTAGINACEAE
  - Plantago aristata
  - Plantago virginica
- RUBIACEAE
  - Diodia teres
  - Galium aparine
  - Galium obtusum
  - Houstonia minima
- CAPRIFOLIACEAE
  - Symphoricarpos orbiculatus
- VALERIANACEAE
  - Valerianella radiata
- CAMPANULACEAE
  - Lobelia spicata
  - Specularia perfoliata
- COMPOSITAE
  - Achillea millefolium
  - Ambrosia artemisiifolia var. elatior
  - Ambrosia bidentata
  - Ambrosia trifida
  - Antennaria neglecta
  - Aster ericoides
  - Aster paludosus subsp. hemisphericus
  - Aster pilosus var. demotus
  - Aster praealtus
  - Bidens polylepis var. retrorsa
  - Boltonia asteroides var. latisquama
  - Boltonia asteroides var. recognita
  - Cacalia tuberosa
  - Cirsium altissimum
  - Coreopsis grandiflora
  - Erechtites hieracifolia
  - Erigeron canadensis
  - Erigeron strigosus
  - Erigeron tenuis
  - Eupatorium perfoliatum
  - Eupatorium serotinum
  - Gnaphalium obtusifolium
  - Gutierrezia dracunculoides
  - Helenium flexuosum
  - Helianthus grosseserratus
  - Helianthus mollis
  - Hieracium longipilum
  - Krigia dandelion
  - Lactuca canadensis var. canadensis
  - Lactuca canadensis var. latifolia
  - Lactuca scariola
  - Liatris asper
  - Liatris pycnostachya
  - Parthenium integrifolium
  - Prenanthes aspera
  - Rudbeckia hirta var. pulcherrima
  - Serenia oppositifolia
  - Solidago altissima
  - Solidago gymnospermoides
  - Solidago missouriensis var. fasciculata
  - Solidago nemoralis
  - Solidago rigida
  - Vernonia baldwini var. interior
  - Vernonia crinita
  - Vernonia fasciculata
  - Vernonia missurica
  - Xanthium chinense

BRYOPHYTES OF AN OPEN TALLGRASS PRAIRIE IN SOUTHWESTERN MISSOURI

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Abstract. A study of bryophytes in an open tallgrass prairie was made between June 1980 and May 1981. Nine species were collected from 5 sample areas. Sample area 1 had the highest % available light and lowest % soil water-holding capacity due to a prior burn. Sample area 3 had the lowest % available light and the highest % soil water-holding capacity. Soil *p*H showed little variation throughout the 5 sample areas. Statistical comparisons suggest that 2 bryophytic communities exist, 1 dominated by *Campylium hispidulum* and the other by *Bryoandersonia illecebra.*

INTRODUCTION

In 1944 Henry S. Conard wrote, "There is no moss among the grasses of the Tallgrass Prairies or the Shortgrass Plains. Moist spots or bare spots or wooded spots among these Plant Associations have their mosses." Since this time a number of papers have published lists of mosses collected specifically from tallgrass prairies (see Timme 1982 for a review). Of the papers, only Duncan (1959) discusses a quantitative ecological study of bryophytes in tallgrass prairie. As another ecological contribution, I studied bryophytes in an open tallgrass prairie in southwestern Missouri.

La Petite Gemme Prairie, owned by the Missouri Prairie Foundation, is a 15-ha upland prairie in Polk County, Missouri, located in the SW¼, NW¼, Sec. 25, T33N, R23W of the Bolivar 7.5-minute quadrangle. The prairie is within the Springfield Plateau near the western edge of the Ozark Province.

The soils of the western 3.25 ha were derived from Mississippian limestone of the Northview Formation (Anderson 1979). The soils of the remaining portion of the prairie are primarily from Cotter and/or Jefferson City dolomites of the Ordovician Period (Anderson 1979). The soils derived from Cotter and/or Jefferson City dolomites have embedded fragments of St. Peter sandstone (Miller 1981, pers. comm.). Where the dolomites have eroded away, the sandstones are exposed.

The area is characterized by yearly temperatures ranging from 3° C normal minimum to 30° C normal maximum (U.S. Department of Commerce 1968, Wallis 1977). Mean annual precipitation is 107 cm with three-fourths coming in the spring (Wallis 1977).

The vascular flora of La Petite Gemme Prairie is diverse. Since its purchase in 1974 some 40 species of grasses, 130 species of forbs, and 8 species of woody plants have been identified (Budde 1978, Timme 1982).

METHODS

Five areas with 5 sites each were chosen to sample, based on elevational differences (Fig. 1), using the line-intercept transect technique (Canfield 1941) modified slightly to use a nylon cord instead of a 1-cm tape. Hattaway (1980) suggested there would be an inaccuracy in the data using a 1-cm tape since 2 or more bryophyte colonies could occupy this space. Therefore, with the cord in place, a ruler was used to measure the length of line touched by each bryophyte colony. At each site the nylon cord was stretched for 5 m in 4 random directions. Data from the line-intercept method were used to determine absolute cover and frequency, relative cover and frequency, and importance values (Greig-Smith 1967). Importance values were then used to construct a bryophyte index of similarity (Whittaker 1975) by area.

At each site, light intensity was measured and soil samples were collected; later, soil water-holding capacity and soil *p*H were determined.

Nomenclature for mosses follows Crum and Anderson (1981). Voucher specimens for each species are deposited in the Ozark Regional Herbarium (SMS) at Southwest Missouri State University.

Analysis of variance and Duncan's multiple range test follow SAS procedures (Helwig and Council 1979).

RESULTS AND DISUCSSION

Physical factors for soil water-holding capacity, available light at the soil surface and soil *p*H are given in Table 1.

A total of 9 species was collected, as follows (numbers in parentheses indicate the sample areas where each species was collected):

Fissidens cristatus (2,3,4,5)
Ditrichum pallidum (2,3)
Weissia controversa (2,5)
Bryum pseudotriquetrum (4,5)

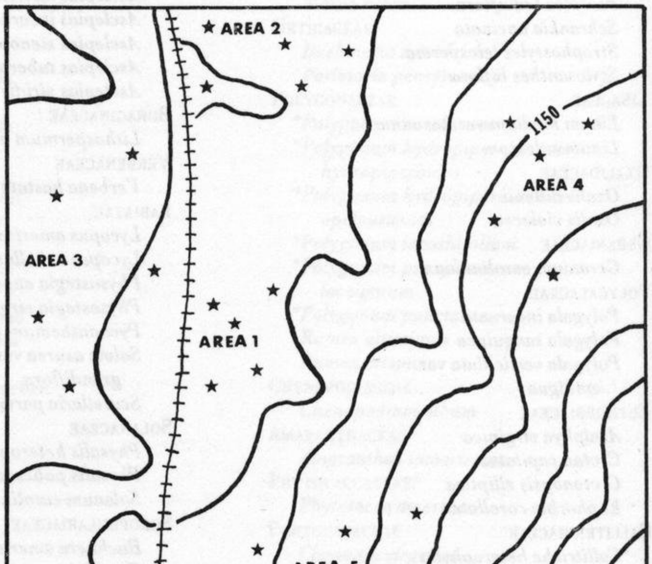

FIG. 1. Map of La Petite Gemme Prairie showing location of sample areas and sites (stars).

TABLE 1. Physical factors at La Petite Gemme Prairie. Values are means, with extremes in parentheses.

	AREA				
FACTOR	1	2	3	4	5
Light intensity (% full sunlight)	100	7 (4-9)	3 (2-4)	7 (5-11)	7 (3-18)
Soil water-holding capacity (%)	75 (58-90)	87 (74-93)	107 (98-120)	88 (79-107)	92 (82-98)
Soil *p*H	6.4 (6.2-6.6)	6.1 (5.9-6.6)	6.0 (6.0-6.2)	6.4 (6.2-6.6)	6.2 (6.0-6.4)

Campylium hispidulum (1,2,3,4,5)
Brachythecium oxycladon (3)
Eurphynchium pulchellum (1,2,4)
Bryoandersonia illecebra (1,3)
Atrichum angustatum (3,5)

The mean relative cover, relative frequency, and importance value for each sample area are given in Table 2. *Campylium hispidulum* had the greatest importance value in areas 1, 2, 4, and 5. *Bryoandersonia illecebra* had the greatest importance value in area 3. The importance values of other taxa were low (0.474 or less).

Values for the similarity index suggest that areas 1, 2, 4, and 5 had similar bryophyte communities (Table 3). Values also suggest that the bryophyte community of area 3 was not similar to any of the other areas. A computer analysis of variance and Duncan's multiple range test also indicated that areas 1, 2, 4, and 5 were similar to each other but distinct from area 3.

Only 1 species, *Campylium hispidulum*, was common to all sample areas in the prairie. It also had the highest values for cover and frequencies for all areas except area 3 where *Bryoandersonia illecebra* was the characteristic species.

A comparison of the mean importance values of *Campylium hispidulum* in areas 1, 2, 4, and 5 indicated no significant difference. However, there was a statistically significant difference at the 95% confidence level in area 3.

Bryoandersonia illecebra was absent from all areas but 1 and 3. A statistically significant difference was found when the mean importance values for this species were compared between the 2 areas. There was also a statistically significant difference between areas 2, 4, and 5 and area 3 for *Fissidens cristatus.* There was no statistically significant difference between the mean importance values of other taxa in the sample areas. The foregoing data suggest that there are 2 communities of bryophytes within La Petite Gemme Prairie. One is dominated by *Campylium hispidulum* and the other by *Bryoandersonia illecebra.*

An examination of the habitat of the *Bryoandersonia illecebra* community revealed a number of significant differences. When physical characteristics of area 3 were compared to the other 4 areas, it was found to be slightly lower in elevation, with high water-holding capacity, high litter accumulation, and low available light at the soil surface. Except for the elevational difference, the other conditions were consistent with the forest habitat one would encounter for *Bryoandersonia illecebra.*

ACKNOWLEDGMENTS

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TABLE 2. Species mean relative coverage (RC), relative frequency (RF), and importance values (IV) for each sample area.

	Campylium hispidulum			*Bryoandersonia illecebra*			*Fissidens cristaus*			*Atrichum angustatum*			*Eurphynchium pulchellum*			*Ditrichum pallidum*			*Weissia controversa*			*Bryum pseudotriquetrum*			*Brachytecium oxycladon*		
AREA	RC	RF	IV	RC	RF	IV	RC	RF	IV	RC	RF	IV	RC	RF	IV	RC	RF	IV	RC	RF	IV	RC	RF	IV	RC	RF	IV
1	.848	.876	1.742	.051	.038	.089							.100	.085	.184												
2	.951	.841	1.792				.035	.134	.168				.003	.006	.010	.005	.010	.016	.003	.006	.010						
3	.061	.166	.226	.933	.744	1.678	.001	.011	.010	.001	.005	.004				.001	.047	.048							.002	.023	.026
4	.705	.783	1.484				.287	.188	.474				.003	.009	.012							.006	.017	.002			
5	.800	.712	1.510				.103	.133	.236	.072	.113	.186							.012	.028	.040	.008	.014	.022			

TABLE 3. Bryophyte index of similarity by area.*

	Area				
Area	1	2	3	4	5
1		0.88	0.14	0.77	0.77
2			0.13	0.84	0.85
3				0.12	0.12
4					0.87
5					

* Possible values range from zero (no similarity) to 1.00 (complete milarity).

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THE EASTERN PRAIRIE-FOREST TRANSITION — AN OVERVIEW

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Abstract. The prairie-forest transition zone is ecotonal in nature and extends as a broad arc along the eastern edge of the mixed and tallgrass prairies from the Canadian Provinces of Alberta, Saskatchewan, and Manitoba southward into Texas. The width of this zone varies in an east-west direction and delineation of the transitional area must be based upon somewhat arbitrary criteria. Western portions of the zone have prairies as the dominant vegetation and forest communities are restricted to favorable microhabitats; on the eastern edge, grasslands are local, isolated outliers in forest. There is a gradual change in climatic patterns from those suitable for grassland species on the western edge to conditions of higher P/E (precipitation/evaporation) ratios, increased humidity and rainfall, and other conditions favoring the growth of trees over that of grasses on the eastern edge. Within this transitional zone, boundaries separating grassland from forest may be gradual or abrupt depending upon local environmental conditions related to topography and soils.

Historically, the position of this transition zone changed with shifting climatic patterns which favored either forests or grasslands. Published studies have documented the current importance of fire as a factor in sustaining grasslands on many sites. Fire cessation across the extend of this zone has resulted in the encroachment of woody species into grasslands and development of closed forests from savannas. No single environmental factor or consistent combination of factors explains the mosaic pattern of forests, prairies, and savannas characterizing the vegetation throughout the transition zone.

INTRODUCTION

The major North American grassland is triangular in shape with the base of the triangle paralleling the foot-hills of the Rocky Mountains from Saskatchewan, Canada, through New Mexico and then extending into southeast Texas. The point of the triangle, the Prairie Peninsula of Transeau (1935), extends into the Midwest with scattered outliers of prairie occurring within a forested landscape eastward into Ohio.

The Rocky Mountains intercept moist air masses from the Pacific Coast and the grassland lies in the rain shadow to the east. From west to east in this grassland the influence of the rain shadow lessens, and the dominance of humid, unstable air masses originating in the Gulf of Mexico increases. Associated with these changes, rainfall increases from 25-38 cm in the western portions of the grassland to 75-100 cm on the eastern edge, potential evaporation decreases, number of days with rainfall increases, and periodic drought and periods of low relative humidity during July and August decrease. Also, from south to north within the grassland, snow cover during winter becomes more continuous (Transeau 1935, Borchert 1950, Risser et al. 1981).

As a result of the continual change in climatic patterns from west to east there is a concomitant shift in the grassland species dominating the vegetation. Ecologists traditionally recognized 3 major grassland divisions. The western shortgrass prairie is dominated by grass species that reach 30-45 cm in height including buffalo grass (*Buchloe dactyloides*), blue grama grass (*Bouteloua gracilis*), and hairy grama grass (*B. hirsuta*). The eastern portion is the tallgrass prairie where the dominant species are 1.8-3.6 m in height and include big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), and prairie switchgrass (*Panicum virgatum*). Occupying areas with effective precipitation patterns intermediate to the tall and shortgrass prairies is the mixed grass prairie, a mixture of tall and short grasses. Tall grasses are abundant in locally moist areas and short grasses are dominant in the locally arid habitats. The mixed grasslands also includes some species which are dominant in the mixed grassland but are less important in the tall and shortgrass prairies. These include needle grasses, e.g., porcupine needlegrass, *Stipa spartea*, and needle-and-thread, *Stipa comata*, and wheat

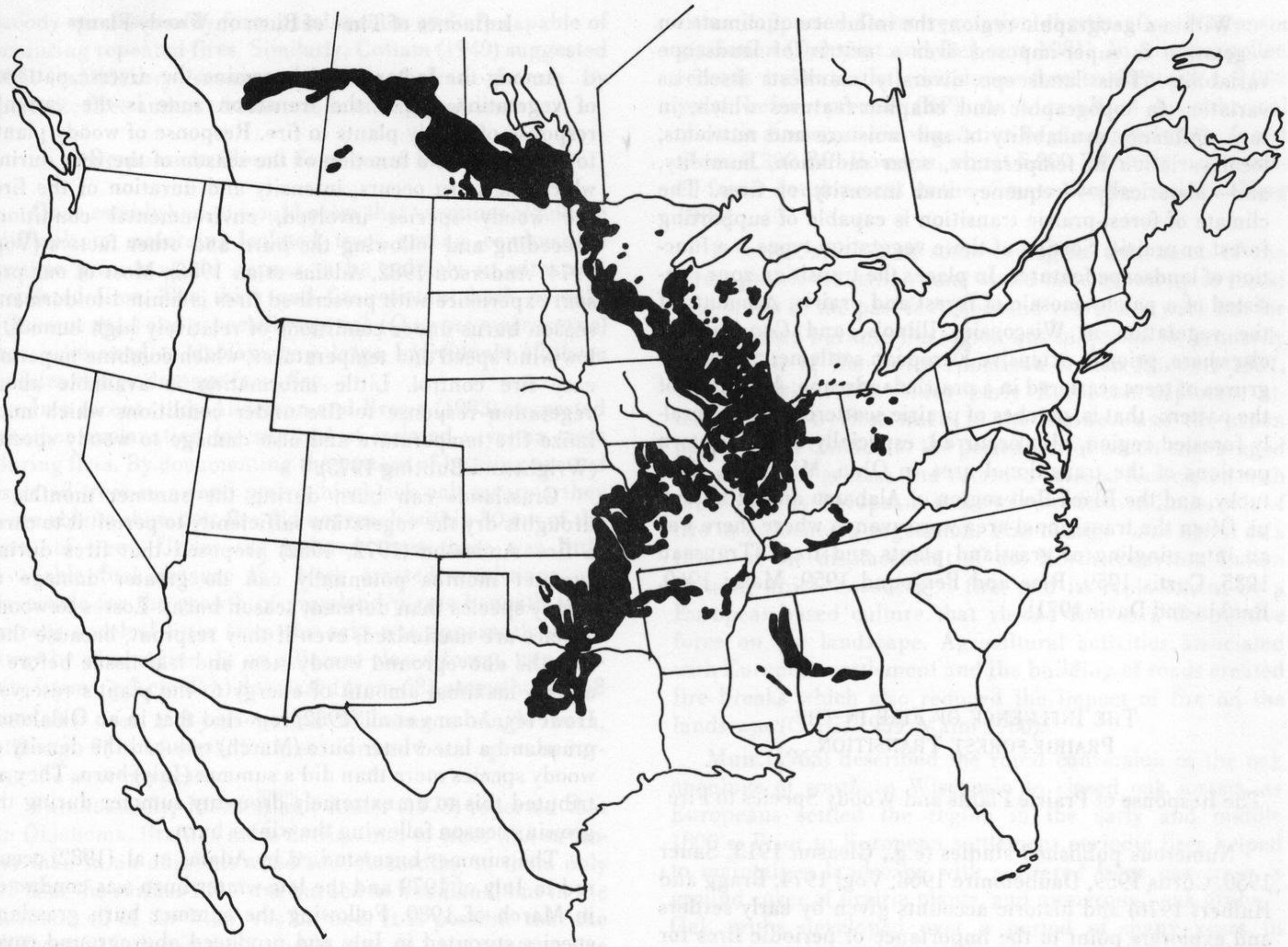

FIG. 1. The eastern prairie-forest transition. The location of the transitional zone was based on several sources but primarily the following references: Marschner (1930), Transeau (1935), Maini (1960), Küchler (1964), Hanson (1965), Risser et al. 1981), and Rowe (1959).

grasses, e.g., western wheatgrass, *Agropyron smithii,* and thickspike wheatgrass, *A. dasystachum,* which are dominant species in the northern portions of the mixed grassland. Southward, little bluestem (*Schizachryium scoparium*) and the grama grasses (*Bouteloua gracilis, B. curtipendula,* and *B. hirsuta*) become increasingly dominant (Weaver 1954, Risser et al. 1981).

The prairie-forest transition is crescent shaped and occurs between predominantly grassland vegetation and areas supporting continuous forest (Fig. 1). In the north the transition is between the mixed grasslands of Alberta, Saskatchewan, and Manitoba and the boreal forest and is called aspen parkland. Southward, the transition extends along the tallgrass prairie from Minnesota through the Midwest and into southeast Texas where it forms the transition to oak-hickory forests.

East of the tallgrass prairie, and north and east of the mixed-grass prairie in Canada, the climate becomes effectively more moist and increasingly favorable for development of forest vegetation. In general, tree species of eastern and central North America are less well adapted to arid climates than are grassland plants. The adaptation of grassland species lies, in part, in their ability to die down to underground organs during periods of prolonged drought, exposing only dead tops above ground (Gleason 1922). Many grass species also have features permitting them to cope with high moisture stress such as (1) bulliform cells which, when they lose water, cause leaf margins to enroll, thereby reducing evaporative surfaces, (2) C_4, or Hatch, photosynthetic pathway, an adaptation associated with plants occurring in areas with high temperature, high solar radiation, and periods of moisture stress (Terri and Stowe 1976, Doliner and Jellife 1979, Redmann and Reekie 1982), and (3) the ability to grow under conditions of low soil-water potential. For example, blue grama grass is able to grow until soil-water potentials of between −40 to −60 bars are reached (Ares 1976, Briske and Wilson 1978).

The C_3 grass species maximize growth under relatively cool and moist conditions and are "cool season grasses," such as Canadian rye (*Elymus canadensis*), or northern grasses (north of 45° latitude) including *Fescue* and *Stipa* spp. They are less well adapted to drought than southern grasses and "warm-season grasses" including the bluestems, grama grasses, Indian grass, and switchgrass, which maximize their growth in mid-summer when droughts are most likely to occur (Williams and Markley 1973, Ehleringer 1978).

Within a geographic region, the influence of climate on vegetation is super-imposed over a matrix of landscape variability. This landscape diversity manifests itself as variation in topographic and edaphic features which, in turn, influence availability of soil moisture and nutrients, local variation in temperature, solar radiation, humidity, and—historically—frequency and intensity of fires. The climate of forest-prairie transition is capable of supporting forest or prairie. Sorting of these vegetation types is a function of landscape features. In places the transition zone consisted of a patchy mosaic of forest and prairie. Accounts of the vegetation in Wisconsin, Illinois, and Canada and elsewhere, prior to extensive European settlement, describe groves of trees scattered in a prairie landscape. A reversal of the pattern, that is, patches of prairie scattered in a generally forested region, also occurred, especially in the eastern portions of the transitional area in Ohio, Michigan, Kentucky, and the Black Belt region of Alabama and Mississippi. Often the transitional area was savanna where there was an intermingling of grassland plants and trees (Transeau 1935, Curtis 1959, Rice and Penfound 1959, Maini 1960, Rankin and Davis 1971).

THE INFLUENCE OF FIRE IN THE PRAIRIE-FOREST TRANSITION

The Response of Prairie Plants and Woody Species to Fire

Numerous published studies (e.g., Gleason 1913, Sauer 1950, Curtis 1959, Daubenmire 1968, Vogl 1974, Bragg and Hulbert 1976) and historic accounts given by early settlers and explorers point to the importance of periodic fires for maintenance of grasslands and savannas under climatic conditions capable of supporting woody vegetation. Grasslands are adapted to periodic fires and evolved in landscapes and under climates which encouraged fires. Landscapes occupied by grasslands are level to gently rolling (i.e., they have few fire breaks) and the climates have periodic drought during which time the vegetation dries and becomes capable of supporting fires. Grasses also tend to encourage fire because they form a finely divided fuel which readily dries and is quickly ignited (Sauer 1950, Anderson 1982).

Adaptations which permit grassland plants to withstand droughts also provide protection during fires. These adaptations are manifested in their herbaceous habit and the occurrence of perennating organs beneath the soil surface. Only dead annual tops are exposed aboveground during droughts or at other times during the year when the grasses are dormant (Gleason 1922, Sauer 1950).

Grassland fires can occur whenever the vegetation is dried sufficiently to burn but they are most likely to occur during droughts or periods of dormancy. During grassland fires, soil surfaces reach temperatures ranging from 83 to 680°C (Wright 1973, Rice and Parenti 1978). But soil is a good insulator, so heat does not penetrate deeply into the soil and grassland species are protected from the fire. In contrast, woody plants can be severely damaged by fire. Fires can kill these plants or destroy their shoots and even though resprouting occurs several years of production are lost.

Influence of Time of Burn on Woody Plants

Among the factors that determine the diverse patterns of vegetation within the transition zone is the variable response of woody plants to fire. Response of woody plants to fire varies as a function of the season of the year during which the burn occurs, intensity and duration of the fire, the woody species involved, environmental conditions preceding and following the burn and other factors (Vogl 1974, Anderson 1982, Adams et al. 1982). Most of our present experience with prescribed fires is limited to dormant-season burns under conditions of relatively high humidity, low wind speed and temperatures, which combine to permit easy fire control. Little information is available about vegetation response to fire under conditions which maximize fire temperature and also damage to woody species (Wright and Bunting 1975).

Grasslands can burn during the summer months, if droughts dry the vegetation sufficiently to permit it to carry a fire. Anderson (1972, 1982) proposed that fires during summer months potentially can do greater damage to woody species than dormant season burns. Losses to woody species are maximized, even if they resprout, because they lose the aboveground woody stem and leaf tissue before it adds a maximal amount of energy to the plant's reserves. However, Adams et al. (1982) reported that in an Oklahoma grassland a late-winter burn (March) reduced the density of woody species more than did a summer (July) burn. They attributed this to an extremely droughty summer during the growing season following the winter burn.

The summer burn studied by Adams et al. (1982) occurred in July of 1979 and the late-winter burn was conducted in March of 1980. Following the summer burn grassland species sprouted in July and produced aboveground cover that could have reduced soil moisture losses in the winter months and during the early part of the next growing season. The late-winter site was bare following the burn until new growth protected the soil surface. These conditions might have made the late-winter burn site drier than the summer burn site for the early part of the growing season and this may have enhanced woody plant mortality on the late-winter burn.

Thus, there are likely complex interactions between patterns of fire and climate of which we understand very little. The difficulty associated with controlling woody invaders into some grassland preserves at the present time (Nelson 1982), even though they are periodically burned, may relate to a lack of creativity in applying fire as a management tool and random climatic events preceding and following the burn.

Mesic and Xeric Woodland Responses to Fire

The ability of woody species to form basal sprouts following a burn and the degree to which the bark provides protection from fire are important factors determining woody plant response to burning. For example, Curtis (1959) suggested that fires through mesic forest (dominated by maples, ashes, elms, etc.) could convert it to a prairie because the dominant tree species are unable to withstand frequent fires. In contrast, a fire through a xeric oak-hickory forest may convert it to a savanna because the woody species readily form basal sprouts and are capable of enduring repeated fires. Similarly, Cottam (1949) suggested that oak-hickory savannas developed from forests by periodic fires and not from trees invading prairies.

Response in Closed Forests and Savannas

Once established, it would seem that savannas would be difficult to maintain. Isolated trees among combustible prairie grasses would appear to be unlikely to withstand repeated fires. The thick and fire-resistant bark of oaks (*Quercus* spp.) and especially bur oak (*Quercus macrocarpa*) has been used to explain how large individuals of these species escape damage from fire.

In a recent study Anderson and Brown (1983) suggested another explanation for survival of isolated savanna trees during fires. By documenting the pattern of burning around isolated trees in a sand prairie-blackjack oak savanna they were able to show that fire did not reach within 30 cm of the base of trees. Under the isolated trees there was little available fuel because the trees created conditions unfavorable for the growth of grassland plants beneath their crowns and leaf litter from the oaks was apparently swept away by wind action. In an adjacent closed forest, tree density (stems $\geq$ 9 cm dbh) decreased from 683 stems/ha to 358 stems/ha over a 3-year period following a single burn, although 75% of top-killed trees formed basal sprouts during the next two years.

Paradoxically, Johnson and Risser (1975) reported that in Oklahoma, fire was more detrimental to trees in a savanna than in an adjacent woodland. According to them only 45% of the surface litter was burned in woodland, but in the savanna all of the litter was burned. It is possible that the differences found in the 2 studies may, in part, relate to size of the trees in the savanna. Small trees would not reduce grass cover beneath their crowns, whereas large savanna trees would provide sufficient competition to substantially reduce or eliminate grass cover beneath their crowns. In the Brown and Anderson study, the average tree was 47 cm in diameter at breast height (dbh) and all trees were larger than 35 cm dbh. Johnson and Risser (1975) reported that aboveground parts of most trees up to 4 cm dbh were killed, and some small trees up to 9 cm dbh were killed or severely damaged. Thus, the small size of the trees in the Oklahoma study may have permitted considerable grass fuel to accumulate beneath their crowns.

The intensity of fires is strongly influenced by factors such as wind speed, temperature, relative humidity, and the dryness of the fuel. I have observed fires which carried well across exposed grassland areas but stopped or burned poorly when they reached adjacent forests where humidity, temperature, and fuel moisture conditions were apparently less favorable for burning. This may explain why the fire burned well through savanna but not the forest in the study reported by Johnson and Risser (1975).

POSTGLACIAL HISTORY OF THE PRAIRIE-FOREST TRANSITION

The long-term vegetational history of a region will be necessarily incomplete and fragmentary, but studies of pollen deposits indicate that much of the prairie-forest transition supported forest vegetation shortly after Wisconsin glaciation (Delcourt and Delcourt 1981). In Illinois, pollen records indicate that deciduous forests dominated 9,000 years before present (BP). As a result of hypsithermal climatic stress, prairie vegetation began replacing the forest about 8,300 BP. However, about 5,000 BP there was renewed forest development as the climate became moister (King 1981).

It is the opinion of some ecologists that much of the forest-prairie transition zone would have grown up to forest vegetation in the past few thousand years, if it were not for the repeated burning the region was subjected to, primarily as a result of the North American Indian (Stewart 1951, 1956, Curtis 1959). Many early European explorers attributed the treeless tracts in the Midwest and the aspen parklands of Canada to the periodic fires which encouraged the growth of grasses and retarded forests. Associated with settlement by Europeans there was a reduction in the role of fire in influencing vegetation. This change came about as a result of the displacement of the North American Indian culture, which encouraged fire, and its replacement by a European-based culture that viewed fire as a destructive force on the landscape. Agricultural activities associated with European settlement and the building of roads created fire breaks which also reduced the impact of fire on the landscape (Curtis 1959, Maini 1960).

Muir (1965) described the rapid conversion of the oak openings of southern Wisconsin to closed oak forests, as Europeans settled the region in the early and middle 1800's. Prior to European settlement periodic fires helped to maintain a landscape with scattered large oak trees, a ground cover of prairie plants, and numerous "oak grubs." Oak grubs developed over a period of many years in response to repeated fires. The aboveground shoots of oaks were repeatedly killed by fires, but the persistent root system continued to develop basal sprouts. The root systems of these "grubs" might be several hundred years old but the relatively small shoot might be only a few years old. The name grub is presumably derived from the German word *graben* which means to hoe or dig, in reference to the methods settlers used to remove these oaks, with their massive root systems, from their fields. When the frequent fires were stopped, as European settlers moved into the region, the grubs quickly gave rise to large shoots and many of the oak openings became closed oak forests. In some of the southern Wisconsin forests it is still possible to discern the large, old, open-grown trees of the oak openings surrounded by forest grown trees, many of which originated at the time of European settlement (Cottam 1949, Curtis 1959).

Along a north-south gradient in Saskatchewan, Maini (1960) reported that the age of the oldest tree in each region revealed that it began growth 10 to 15 years after the introduction of the train. Paradoxically, the advent of railroads initially tended to increase fire frequency, because sparks from the engines set fires; however, the railroads brought in settlers and as more land was put under cultivation fires decreased in frequency.

Maini (1960) also suggests that at the present time aspen reproduction is limited to vegetative methods and that the current aspen (*Populus tremuloides*) groves, which have become larger in recent times, did not result from aspen invading the grasslands, but rather from the growth and spread of aspen that had previously been maintained in a shrubby condition and restricted in distribution as a result of periodic fires. He estimated the spread of aspen into grasslands in Saskatchewan in the absence of fire to be about 30 to 63 cm per year. He also believes that aspen groves resulted from the contraction of a more extensive forested area that existed following glaciation. The forest became restricted to localities where soils and microclimate compensated for climatic unfavorableness following a shift in climate to one that favored grasslands. This pattern is the same as that described for Illinois by King (1981) on the basis of palynological evidence.

ROLE OF TOPOGRAPHY AND DRAINAGE PATTERNS

Topography influences the vegetation of a region by producing varied microclimates, soil and drainage patterns, and also by influencing the frequency and intensity of fires. Wells (1970 a, b) noted that within grasslands escarpments tend to support woody vegetation. This he attributed to reduced fire frequency and intensity on scarps, which act as firebreaks. However, the pattern of forest and grassland vegetation as a function of topography can be quite variable and strongly influenced by other factors.

According to Maini (1960) the aspen groves of the aspen parklands occur in local depressions where the landscape is level and in the southern part of the aspen parkland where the climate more strongly favors grasses than trees. Depressions provide favorable moisture conditions for tree growth and the frequency and intensity of fires is reduced. However, at the northern fringes of the aspen parkland the grasslands are restricted to upland ridges which are dry and favor grasses. Forests occupy the remaining landscape positions.

In the Midwest, Gleason (1913) used original land survey records to demonstrate that forests tended to occur more frequently on the east side of rivers and large bodies of water than on the west sides where prairies were the dominant vegetation. This distributional pattern was attributed to protection from fires that were generally carried from west to east as a result of the prevailing wind direction.

The influence of topography in creating varied microclimates and determining the patterns of fire is illustrated by the presettlement vegetation of central Illinois. During presettlement times, mesic forests dominated by elms (*Ulmus* spp.), ashes (*Fraxinus* spp.) and sugar maple (*Acer saccharum*) were associated with dissected ravines and narrow river flood plains. These sites provided protection from fires and sheltered microclimates with relatively low moisture stress. Uplands adjacent to these sites supported oak forests dominated by white and black oak. The nearly flat to rolling till plains and broad glacial moraines supported tallgrass prairies (Gleason 1922, Rodgers and Anderson 1979).

Oaks are relatively shade intolerant compared to the mesic species. Prior to European settlement, occasional fires in the sites they occupied prevented invasion of shade-tolerant but fire-sensitive mesophytes and also encouraged oak regeneration (Rodgers and Anderson 1979). However, with the cessation of fires, resulting from extensive agriculture development in the middle of the 19th century, the oak forest sites were invaded by white ash (*F. americana*), American and red elms (*Ulmus americana, U. rubra*), and sugar maple. The increased shade and competition in the oak forests resulting from invasion of these species has substantially reduced oak reproduction. In the current oak forests, white, black and red oaks (*Quercus alba, Q. velutina,* and *Q. rubra*) dominate the canopy, but these species are nearly absent from the reproductive strata. The shade-tolerant mesophytes will, in the next 50-100 years, replace the oaks as they are removed from the canopy through natural mortality. This change in forest composition illustrates how fire, climate and topography interacted in presettlement time to produce a vegetational pattern and how this pattern has been altered by elimination of fire (Anderson and Adams 1978, Adams and Anderson 1980).

ROLE OF SOILS

Within the transition the primary influence of soil appears to be related to its importance in determining available water. In general, fine-textured soils hold more moisture than sandy soils. However, for a variety of reasons fine-textured soils can be unfavorable for tree growth and more suitable for grasslands because of low moisture availability at certain times during the year.

In southern Illinois, a mostly forested region, post oak (*Q. stellata*) savannas developed on fine-textured soils with clay pans. Pans develop in some soils at depths of about 60 cm (Fehrenbacher and Odell 1959) and prevent water movement deep into the profile. Moisture storage is limited to the area above the clay pan and root growth is also often limited to the zone above the pan. During the spirng the soil can be completely saturated because of impeded water movement above the pan. However, because of a water-storage capacity limited to the depth of the pan, soils are extremely droughty by mid-summer. Apparently, these conditions of alternating saturation and extreme drought are more conducive to development of savannas, containing grassland species and a few tree species such as honey locust (*Gleditsia triacanthos*), pin oak (*Quercus palustris*) and post oak, than of closed forest (Anderson and Anderson 1975).

The crosstimbers is also a region where vegetation patterns appear to be related to soil texture. Today the crosstimbers is a band of timbered land dominated by post and blackjack oak (*Q. marilandica*) extending in a north-south direction from southern Kansas through Oklahoma and Texas. Various authors have described this vegetation as varying from 10-90 km in width to as much as 180 km (Risser et al. 1981).

Historically, the region was a mixture of oak savanna and closed oak forests dominated by post and blackjack oak. Prairie grasses (little bluestem and Indian grass) were the dominant understory species. However, cessation of fire and grazing in recent years resulted in a shift towards a dominance of annual grasses and forbs. Elimination of fire from this vegetation also resulted in the development of a closed oak forest community, with thick litter accumulations and little understory vegetation, from the savannas.

In Oklahoma, Rice and Penfound (1959) concluded that within the crosstimbers region, forests develop on shallow, coarse-textured soils and adjacent prairies occur on fine-textured soils. Using GLO survey records, Bell and Hulbert

(1974) demonstrated that in Kansas separation of forest and prairie occurred on the basis of soil texture in presettlement times. The reason for this separation due to soil texture has not been fully explained. However, under certain conditions, coarse textured soils may provide more moisture to plants than fine-textured soils. For example, if soils are dried to very low levels of moisture, light showers may recharge coarse textured soils with their low water-holding capacity; whereas, the same amount of precipitation may be insufficient to recharge fine texture soils to the point where additional water is made available to plants. Also, clay-pan soils, with their limited water storage capacity, develop in fine-textured soil but not in coarse textured ones.

Similarly, in the Black Belt prairie (Rankin and Davis 1971), a crescent-shaped area extending from central Alabama into western Mississippi, prairies occur on fine textured soil. These soils are characterized "by seasonal droughts that preclude well-developed forests but are characteristic of grasslands" (Risser et al. 1981).

CONCLUSIONS

The historic shift of climatic patterns, variation in microclimates caused by topography, varied frequency and intensities of fires, edaphic factors, and the influence of human activities resulted in the diverse mixture of grassland, forest, and savanna vegetation that characterizes the prairie-forest transition. A careful consideration of this vegetation results in the realization that we have only begun to understand the nature of the transiton. Factors such as the importance of oak wilt (Kline 1982) and browsing animals, such as elk (*Cervus canadensis*) in retarding tree growth are only poorly understood. The nearly universal acceptance that fire controls woody species and encourages grasslands needs to be re-examined with the realization that fire does not operate independently on the vegetation. The response of vegetation to fire is a function of species composition, the season of the burn, fluctuating climatic cycles, which include periodic drought, and other factors.

Britton and Messenger (1969) suggested that the nature of the drought is important in determining its influence on woody vegetation. They presented data to show that during the drought years of 1933 and 1934, when there were large numbers of trees killed within the Prairie Peninsula, the general region of the Prairie Peninsula did not experience soil-moisture recharge between the summer of 1933 and the summer of 1934. In contrast, soil-moisture recharge occurred in adjacent forested areas. They concluded that this type of drought is more detrimental to trees than grasses because trees have deeper root systems than grasses and the trees benefit from deep soil moisture recharge. Grasses with their shallow, but extensive, root systems near the surface can utilize the moisture in the upper soil layers more effectively than trees and are less dependent than trees on deep recharge of the soil moisture.

Within the transitional zone no single set of environmental factors explains the mosaic pattern of vegetation. The environmental factors influencing the vegetation operate in concert, with the relative importance of each factor and the interactions of the factors varying in time and space.

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PRELIMINARY OBSERVATIONS ON THE DISTRIBUTION AND ECOLOGY OF TALLGRASS PRAIRIE IN SOUTHERN ONTARIO

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Abstract. The prairie peninsula, as originally defined by Transeau, shows northeastward extensions into the western part of Ohio and southern Michigan. Recent investigations of the vegetation of Ontario indicate tallgrass prairie extends into southwestern Ontario and may possibly have spread further east. This paper examines the ecology of the tallgrass prairie and related sites in southern Ontario, especially species composition and structure in relation to soil, climatic, and disturbance factors. Particular reference is given to soil types in the region, and some of the related factors affecting prairie species is assessed. Dominant species in tallgrass and related grassland communities are described and their relationship to other communities in the region is discussed.

INTRODUCTION

Early discussions of northeastward extensions of the prairie peninsula focused on Indiana, Ohio, and Michigan (Veatch 1927, Transeau 1935, Parker 1936, Thompson 1939, Jones 1944). Further studies of these areas have shown prairies to be more extensive than originally thought, including some very extensive and well-developed prairie communities in the Ontario-Michigan border region (Hayes 1964, Rodgers 1966, Thompson 1975).

Historical records point to the presence of these communities prior to 1800. Lumsden (1966) and Pratt (1979) cite several survey records dating from 1679 to 1847 that show tracts of land described as "fine, open plains," "extensive natural meadows," and "prairie" may have covered an area in southwestern Ontario totalling 40,000 ha. Farming has removed most of these once extensive prairies, but several localities have been discovered to contain significant remnants.

Many of the species originally occurring in prairie have spread elsewhere in the Great Lakes region of Ontario and form, with other species, prairie-related communities. This study looks at the structure, composition, and distribution of tallgrass prairie in southwestern Ontario and discusses their abiotic components—soils, climate, and moisture conditions. While these components comprise only 1 aspect of the environment in which these species occur, they serve as a basis for further understanding these communities.

RESEARCH METHODS

Initial work in 1981 involved locating areas suitable for study. Stands were selected on the basis of the physiognomy and presence of dominant prairie species and other floristic features (Weaver and Fitzpatrick 1934, Curtis 1959).

In 1982 the spring flora was checked and, where spring ephemerals were abundant, quadrats were laid to estimate cover. Permanent quadrats were also laid in selected stands to determine changes in cover of various species over the season. Soil pits 0.5 m in depth were dug in all stands to describe soil profiles and to collect soil samples for nutrient, moisture, texture, and organic matter analyses. Stands were also visually assessed for fire and soil disturbance, microclimate, moisture, and other environmental features.

Quantitative vegetation studies included a complete presence list for each stand and randomly laying 15 m² quadrats through the stand to measure frequency, estimate cover of the species, and describe the structure (layers and dominance) of the vegetation.

PHYSIOGRAPHIC FEATURES

Almost all the stands (Fig. 1) are located on sand plains (Chapman and Putnam 1966). The Windsor area is the site of glacial lake deposits, the latest being Lake Rouge, which deposited thin layers of sands and silty clays up to 5 m in depth (Hoffman 1975). Walpole Island (actually 5 small

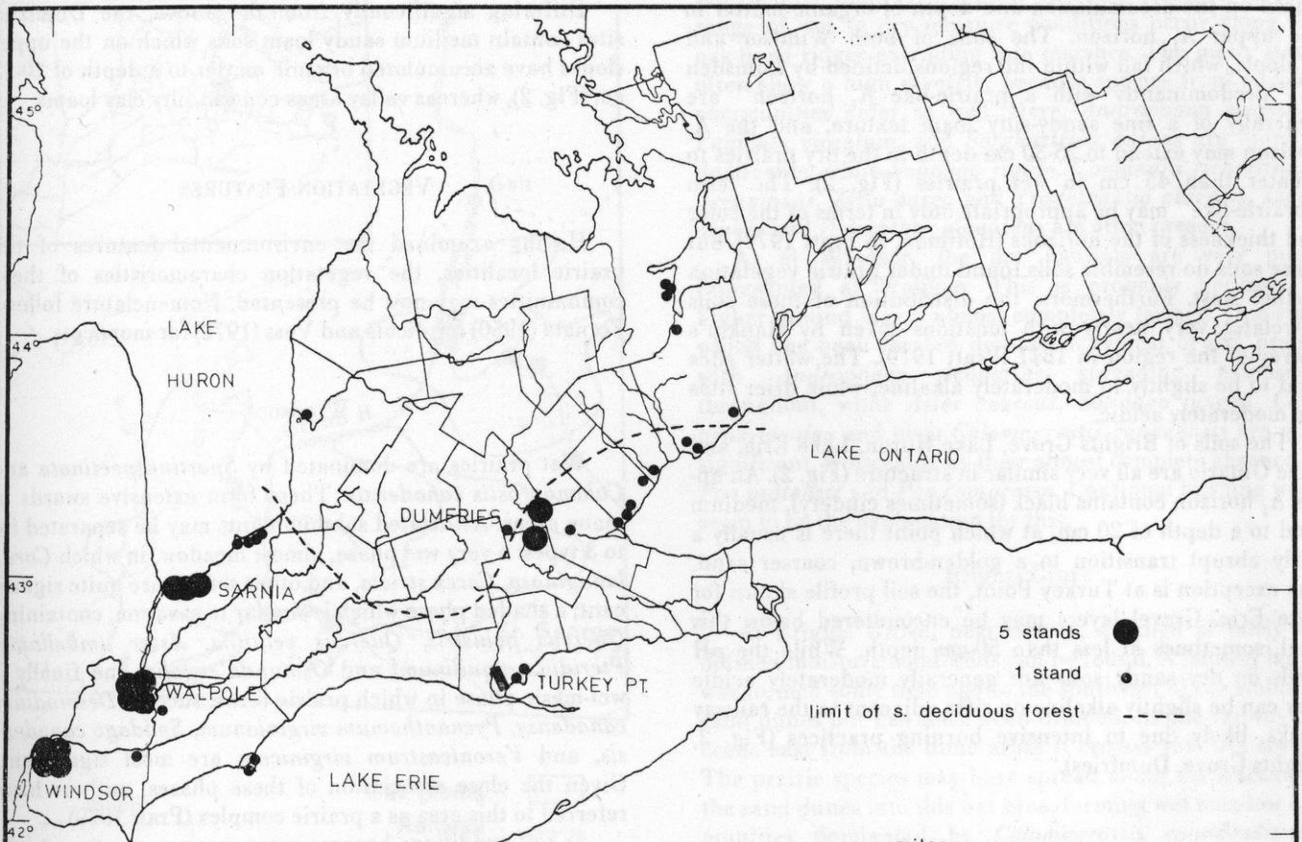

FIG. 1. The distribution of prairie stands studied in southern Ontario.

islands) was formed from deltaic outflows of the St. Clair River and has a significant silt/sand component in the substrate.

The Brights Grove (Sarnia), Lake Huron, Lake Erie, and Lake Ontario areas are part of old beach shorelines and/or stabilized sand dunes. The sand is often coarse and may be underlain with gravel beds. The only exceptions are the Turkey Point stands along Lake Erie, which are part of the Norfolk sand plain. These sands were deposited from spillways of the Galt and Paris moraines, are fine to medium in texture, and may be more than 10 m in depth.

The Dumfries area does not occur on a sand plain. It is located on the Galt and Paris till moraines, which have sandy loam soils often thinly layered over a rocky substrate. Some of the stands are located on rather steep slopes and high ridges. The only other area where slopes occur is Brights Grove, where several small, 10-m-high, dune-like ridges are found along the railway.

A number of stands are located along or near railways, including most of the Brights Grove stands (railway built in 1860), many of the Dumfries stands (built in 1890s), and almost all of the Lake Ontario stands (pre-1900). At these locations, stands were chosen in the least disturbed portions of the right-of-way.

The physiographic features may be summarized as follows: stabilized river deltas, stabilized sand dunes and glacial beach shorelines, and dry till moraine and spillway sites.

CLIMATIC CONDITIONS

Climatic conditions are greatly influenced by the moderating effects of the Great Lakes, such that many shoreline areas are significantly warmer than localities further inland. The majority of our stands occur within the warmest regions of southern Ontario, mostly in the region of 2700 Corn Heat Units of Chapman and Brown (1966). Because 2300 CHUs coincides with the main areas of tallgrass prairie in southeast Manitoba (the only other area in Canada where tallgrass prairie is known to occur) we might expect the major prairie grasses to extend as far north in southern Ontario. Indeed, the distributions of *Andropogon gerardii*, *Andropogon scoparius*, *Panicum virgatum*, *Sorghastrum nutans*, and *Spartina pectinata* (Dore and McNeill 1980) are seen to extend only slightly beyond this zone, although the Canadian Shield, which runs near the 2300 CHU line, may also have a significant effect.

SOIL FEATURES

The soils of certain areas in southwestern Ontario exhibit prairie-like features, according to Lumsden (1966), based on the accumulation and depth of organic matter in the upper A_1 horizon. The soils of both Windsor and Walpole, which fall within the regions defined by Lumsden as "predominantly with a prairie-like A_1 horizon" are generally of a fine sandy-silty loam texture, and the A_1 horizon may extend to 25-30 cm depth in the dry prairies to greater than 45 cm in wet prairies (Fig. 2). The term "prairie-like" may be appropriate only in terms of the color and thickness of the horizons (Hoffman, in Pratt 1979), but these soils do resemble soils found under prairie vegetation further west. Furthermore, the distribution of these soils correlates very nearly with locations given by Rankin's survey of the region in 1847 (Pratt 1979). The wetter sites tend to be slightly to moderately alkaline, while drier sites are moderately acidic.

The soils of Brights Grove, Lake Huron, Lake Erie, and Lake Ontario are all very similar in structure (Fig. 2). An upper A_1 horizon contains black (sometimes cindery), medium sand to a depth of 20 cm, at which point there is usually a fairly abrupt transition to a golden-brown, coarser sand. The exception is at Turkey Point, the soil profile shown for Lake Erie. Gravel layers may be encountered below this level, sometimes at less than 50-cm depth. While the *p*H levels on dry sandy soils are generally moderately acidic they can be slightly alkaline on sites adjacent to the railway tracks, likely due to intensive burning practices (Fig. 2, Brights Grove, Dumfries).

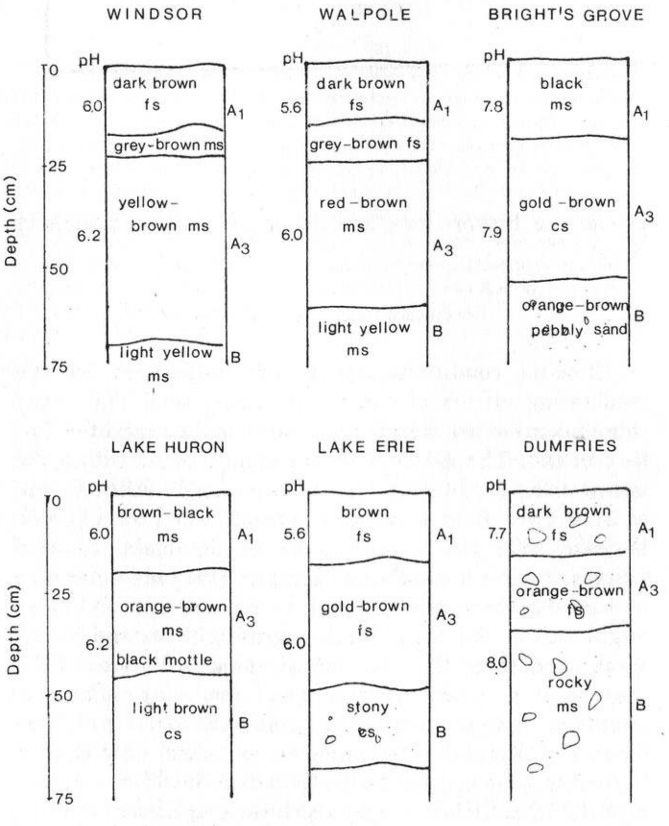

FIG. 2. Comparison of representative soil profile development of dry stands in each of the major areas studied in southern Ontario.

Differing significantly from the above, the Dumfries sites contain medium sandy loam soils which on the upper slopes have accumulated organic matter to a depth of 20-25 cm (Fig. 2), whereas valley areas contain silty clay loams.

VEGETATION FEATURES

Having examined the environmental features of the prairie localities, the vegetation characteristics of these communities may now be presented. Nomenclature follows Fernald (1950) for dicots and Voss (1972) for monocots.

Windsor

Wet prairies are dominated by *Spartina pectinata* and *Calamagrostis canadensis*. These form extensive swards in many areas. Associated subdominants may be separated into 3 types: a very wet phase, almost meadow, in which *Carex lanuginosa, Carex stricta,* and other sedges are quite significant; a shaded phase which is similar to savanna, containing *Quercus palustris, Quercus velutina, Aster umbellatus, Pteridium aquilinum,* and *Osmunda regalis;* and finally a wet-mesic phase in which prairie forbs, such as *Desmodium canadense, Pycnanthemum virginianum, Solidago canadensis,* and *Veronicastrum virginicum* are most significant. Given the close association of these phases, authors have referred to this area as a prairie complex (Pratt 1979).

As soil conditions become more mesic a greater variety of grasses are important dominants, such as *Andropogon gerardii, Panicum virgatum, Poa compressa,* and *Sporobolus asper,* while other grasses, such as *Muhlenbergia frondosa, Calamagrostis canadensis,* and *Sorghastrum nutans* are frequently present. Scattered thickets of *Cornus racemosa, Rhus typhina, Corylus americana,* and *Salix* spp., which occur throughout the prairie-savanna area, are seemingly becoming more prominent.

Dry localities at Windsor are very poorly represented; some of the more common dominants include *Aristida purpurascens, Sorghastrum nutans, Poa compressa, Panicum oligosanthes, Aster ericoides, Euphorbia corollata* and *Lespedeza capitata,* while *Antennaria neglecta* often forms an inconspicuous ground cover. Absent as a dominant is *Andropogon scoparius.*

A unique type of prairie community at Windsor is the forb prairie. Maycock (in Pratt 1979) used this term to describe areas of abandoned farmland which have remained open fields but are dominated by a variety of native forbs. These have strong prairie affinities; for example, *Coreopsis tripteris, Silphium terebinthinaceum, Euphorbia corollata, Scleria triglomerata, Lithospermum canescens, Aster ericoides,* and *Monarda fistulosa* are all present in great abundance. The grasses are only lightly scattered through. It is possible that forb prairie is a transitional phase between old field and tallgrass prairie. Unfortunately it appears that we are also seeing tallgrass prairie at Windsor becoming a transitional phase of oak savanna, since fires have greatly decreased in the last 15-20 years. A regular burning program for the Ojibway Prairie Provincial Nature Reserve in Windsor began in the spring of 1983 in an effort to maintain these prairie communities.

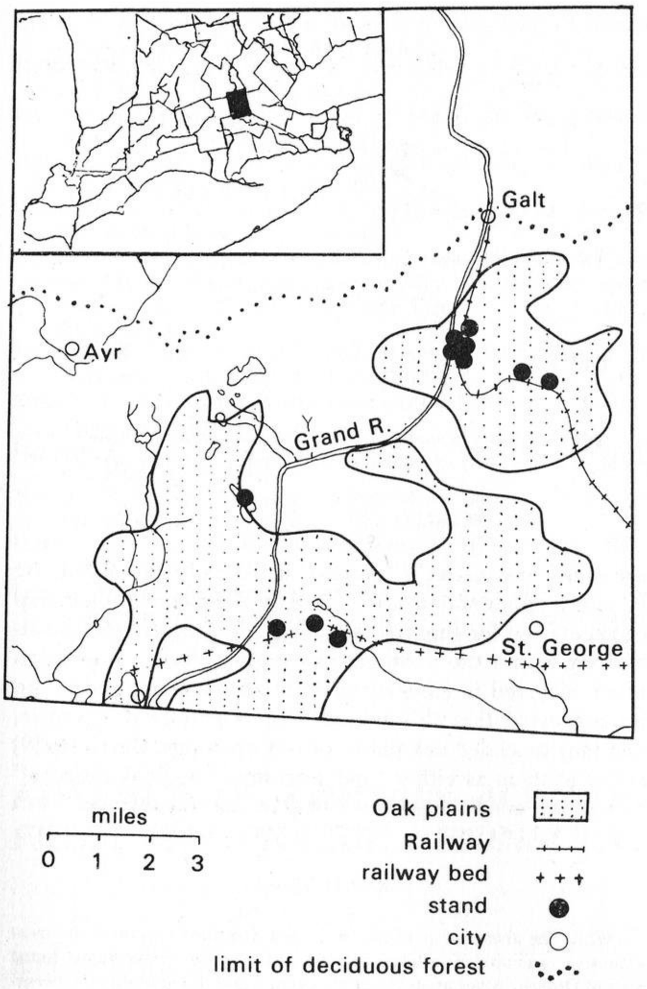

FIG. 3. The occurrence of oak plains in Dumfries Township from Marlett's survey notes (1816-1817) (adapted from Wood 1961). Inset shows the location of Dumfries Township in southern Ontario.

Walpole Island

Walpole Island, an Indian Reserve, contains much the same variety of communities as at Windsor; though it may be less diverse, it is far more extensive. One site exceeds 1,000 acres, and includes mesic prairies, wet prairies, and marshes adjacent to wet oak forests. Continual burning by the Indians has maintained the prairie openings in very good condition.

The wet areas, dominated by *Spartina pectinata* and *Calamagrostis canadensis* show some resemblances to sedge meadows where *Carex stricta, Carex lanuginosa,* and *Carex buxbaumii* are abundant, but more commonly have *Aster simplex, Thelypteris palustris, Convolvulus sepium,* and *Iris virginica* as a significant subdominant layer. *Helenium autumnale* and *Asclepias sullivantii* are frequently present.

Wet-mesic sites show a greater diversity of dominants with *Andropogon gerardii, Sorghastrum nutans,* and *Panicum virgatum* forming extensive swards with *Spartina* sp. and *Calamagrostis* sp. Forbs, such as *Liatris spicata, Desmodium canadense, Pycnanthemum virginianum, Vernonia altissima,* and *Solidago altissima,* are very prominent.

Mesic prairies, while still uncommon, are much better represented than at Windsor. In some localities the full range of wet to dry moisture conditions occur along dry, oak-lined ridges extending into marshes. The mesic stands often show a high diversity because species from adjacent communities enter as well. Here, *Andropogon scoparius, Panicum virgatum,* and *Sorghastrum nutans* are found as dominants, while *Solidago rigida, Comandra richardsiana, decumbens, Zizia aurea* and *Tradescantia ohiensis, Liatris aspera* and *Helianthus giganteus* are often present.

As at Windsor, the dry habitats are very poorly represented at Walpole. This is probably because the higher ground is now almost completely farmed. One stand which has been located does seem typical of dry prairie, with *Andropogon scoparius* spreading extensively throughout, while *Aster azureus, Solidago juncea, Carex pensylvanica* and even *Calamagrostis canadensis* are quite significant. Noticeable by their almost complete absence are *Poa pratensis* and *Poa compressa.* Continual burning would seem to be the explanation for this.

Brights Grove

At Brights Grove, near Sarnia, a range of fairly well defined moisture conditions can be found. A marshy lagoon was formed some time ago to the southeast of the stabilized sand dunes but has since been drained. As the railway proceeds east from the dune areas it crosses this wet section. The prairie species may have spread along the tracks from the sand dunes into this wet area, forming wet meadow communities dominated by *Calamagrostis canadensis* and *Carex stricta* with *Andropogon gerardii, Solidago canadensis, Thalictrum* spp., and *Solidago graminifolia.*

All of the wetter areas are virtually restricted to the railway right-of-way (farms line the tracks on both sides) and have been extensively disturbed by ditch digging. These wet areas are similar in many ways to tallgrass prairie, but are much simpler, and lack many of the significant wet prairie forbs. *Spartina pectinata* is also absent, and *Panicum virgatum* occurs only sporadically.

The dry habitats are well represented here, and occur in clearings in the surrounding oak (*Quercus velutina*) savanna and along the railway line. Many dry prairie forbs, such as *Lespedeza capitata, Solidago rigida, Lithospermum croceum, Euphorbia corollata,* and *Asclepias tuberosa* occur with *Andropogon scoparius, Sorghastrum nutans* and, to a lesser extent, *Stipa spartea, Koeleria macrantha,* and *Panicum oligosanthes. Poa compressa* and *P. pratensis* are also very common. These features suggest that Brights Grove shows characteristics of both sand prairies and tallgrass prairies.

Great Lakes Shoreline

Along the Great Lakes shorelines the grassland communities resemble sand prairies, and are quite similar with respect to their dominants. While much simpler than at Walpole or Windsor, they are comparable to the dry sites at Brights Grove. That is, *Andropogon scoparius, A. gerardii, Poa compressa,* and *Sorghastrum nutans* are commonly found as dominants, while *Carex pensylvanica, Carex foenea, Liatris cylindracea, L. aspera, Asclepias tuberosa, Monarda fistulosa, Lespedeza capitata, Rumex acetosella, Aster laevis, Aster azureus,* and *Solidago nemoralis* are

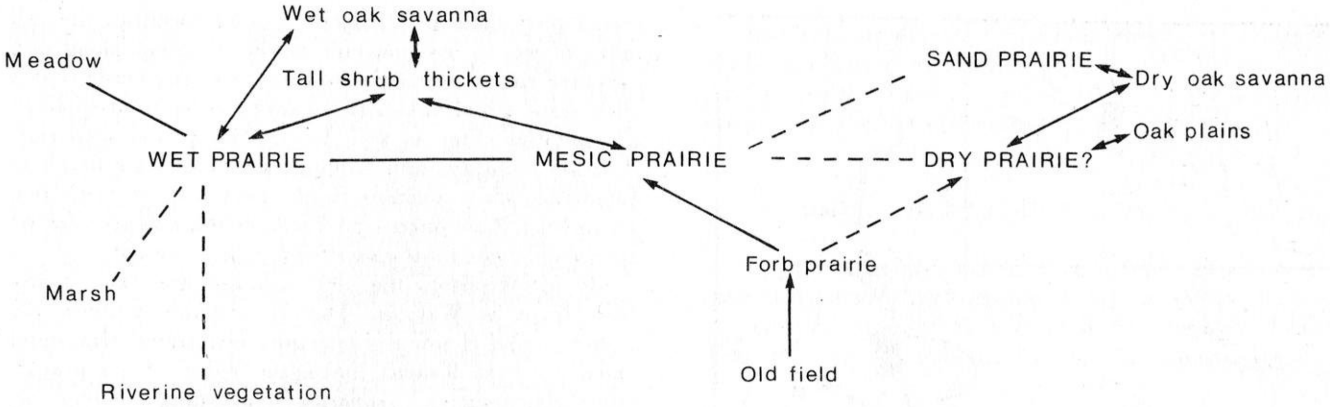

FIG. 4. Diagram indicating possible relationships of communities associated with tallgrass prairie in southern Ontario. Arrows indicate possible directions of succession, solid lines indicate communities often found adjacent to, or more closely resembling, prairie, and broken lines indicate communities less closely resembling prairie.

often present.

This is a rather select set of sand dune stands, since the sites were chosen on the basis of their resemblance to tallgrass prairie vegetation, and may not represent the full variation found in sand prairies (Curtis 1959).

Dumfries

Although a variety of terrain and soil features exist, the range of dominants is small and diversity is comparable to Brights Grove. The area is interesting because of the many prairie-associated species that occur there. *Andropogon gerardii, A. scoparius, Sorghastrum nutans, Poa compressa,* and *P. pratensis* are commonly found as dominants, at times forming almost pure stands along the railway lines. Few forbs are seen until the late summer, when *Aster azureus, Solidago canadensis, Aster ericoides, Solidago juncea, Desmodium canadense, Lespedeza capitata,* and, in more disturbed sites, *Hieracium florentinum, Achillea millefolium,* and *Rubus strigosus* reach their peak. One often finds *Lithospermum canescens, Lithospermum croceum, Euphorbia corollata,* and *Asclepias tuberosa* scattered throughout these areas. *Tradescantia ohiensis,* a more select prairie species, is found here.

While many of the sites are located along abandoned railways, suggesting that fire played an important role in the maintenance of these species, several areas occur on upland oak forest sites near the Grand River. Of particular interest is the restricted occurrence of some prairie species in an abandoned railway bed along the Brand County line (N. and S. Dumfries line). After the grading for the proposed site was completed, the project was abandoned (Fig. 3), leaving an exposed, rocky surface with little soil. Thus the maintenance of prairie species may also result from their ability to colonize poor soils.

What can we make of this inland area? The surrounding vegetation offers some important clues. The area was largely upland oak savanna, in which *Quercus velutina, Quercus ruba,* and *Carya ovata* are dominant, although little remains today (Maycock 1963). Ball (1981) has recently found *Quercus ellipsoidalis* here, a locality 200 km east of the nearest site in Michigan. The original survey of Dumfries township by Marlett in 1816-1817 (Wood 1961) describes certain areas as "oak plains," "plains," or "meadows." When the locations of our stands are plotted on the reconstructed map of vegetation for this township (Fig. 3), they are seen to fit entirely within the "oak plains" region. Prairie vegetation often occurred in association with oak savanna, and it can be suggested that this inland area resembles dry prairie, and may be called oak plains or oak openings. Curtis (1959) refers to them as either "oak openings" or "oak barrens" depending upon the presence of *Quercus ellipsoidalis.*

CONCLUSIONS

While the above areas which have been described represent the most extensive examples of tallgrass prairie in the southern deciduous forest area of Ontario, other areas containing significant, though isolated, occurrences of prairie species continue to be found (Roberts et al. 1977, Reznicek 1980). Unusually extensive prairie sites have also been found in central Ontario (Reznicek 1983). Caution must be exercised in considering these as possible relicts of former tallgrass prairie sites until further evidence of their extensiveness can be documented. Paleoecological evidence points to the existence of many widespread prairie species throughout the prairie-forest border region since the Pleistocene, but which have never been part of any significant prairie assemblage (King 1981). Often recent human disturbances allow prairie species to colonize and dominate a site (Reznicek 1983).

To summarize these comments on the prairie communities of Ontario, a web diagram is presented indicating the possible floristic relationships between these areas (Fig. 4). All the communities are adjacent to oak savanna and may be successionally related to it. The thicket communities, more common in the wetter situations, form scattered, and sometimes extensive clumps through the prairie and savanna. Many of the wet prairie sites grade into either marsh, predominantly *Typha* marsh, or meadow, usually dominated by *Carex* sp. or *Calamagrostis* sp.

Old fields and forb prairies may be successionally related to tallgrass prairie in areas where the prairie is dominant, while sand prairies and oak plains are probably different types of dry communities that resemble tallgrass prairie in certain dominant species. It is not clear how significant a community the dry prairie was in the past. All that remains at present are small isolated sites which are quite disturbed.

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ABSENCE OF CERTAIN AQUATIC VASCULAR PLANTS FROM THE PRAIRIE PENINSULA

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Abstract. Examination of over 450 distribution maps of eastern North American aquatic and wetland vascular plants reveals that at least 22 species occurring more commonly in adjacent regions are rare in or absent from the Prairie Peninsula. These species are generally common in the Middle Atlantic States, more scattered throughout the southern and Mississippi valley lowlands, and extend northward into the western Great Lakes region. In southeastern Missouri they are generally restricted to unglaciated upland sink-hole ponds formed during the last Ozarkian uplift in late Tertiary time. The plants of these ancient relic ponds might have been available for an immediate northward migration following the retreat of the Wisconsin glacier. Their present-day distribution in the glaciated territory of the western Great Lakes region is evidence that this migration occurred. Their absence from the Prairie Peninsula, as suggested by Gleason (1923), may be explained by the warm, dry Xerothermic Period, from 8,000 to 5,000 years BP, when the ponds and shallow lakes would have become dry and the plants would not have survived. The known macrofossil record of *Najas gracillima* supports this viewpoint. Additional confirming evidence should be sought among preserved aquatic plant macrofossils from lake sediments in the region. Most of the species rare in or absent from the Prairie Peninsula are also of waters more acidic than alkaline. This factor may also be of importance since the plants are generally absent from areas underlain by calcareous bedrock, as is evident in Ohio, where the species are much more common in the eastern portion than in the western portion of the state.

INTRODUCTION

The Prairie Peninsula is the name applied to the wedge-shaped projection of prairie biota that extends from the Prairie Province of the Great Plains in central North America eastward from the Mississippi River across most of Illinois and into western Indiana, with outliers in southern Wisconsin, southern Michigan, and as far east as central Ohio. The concept of the Prairie Peninsula was first proposed by Charles C. Adams (1902), the pioneer animal ecologist and biogeographer, who wrote: "From the Great Plains east there is a prairie highway reaching as far east as northern Indiana, and forming some sort of peninsula extending east from the Great Plains into a densely forested region." Adams's concept was further developed by 2 of his students, Henry Allan Gleason and Edgar Nelson Transeau. Gleason (1923) characterized the eastern extension of the Prairie Province on a purely floristic basis in his classic paper, *The Vegetational History of the Middle West*, while Transeau (1935) is identified as providing the name, "Prairie Peninsula," mapping its geographical boundaries, and discussing its climatic characteristics in his often-cited paper, *The Prairie Peninsula.*

The eastern extension of the Prairie Peninsula was considered by both Gleason and Transeau to have been more extensive in the past, having been brought about by a period or periods of prolonged drought conditions in North

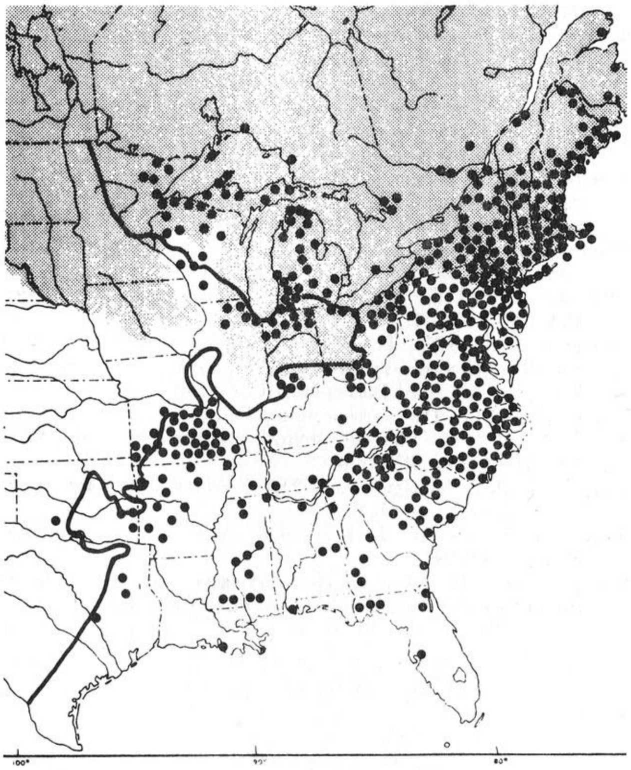

FIG. 1. Map of the distribution of *Sparganium americanum* in eastern North America.

America during either late post-glacial or prehistoric time, or sometime from about 8500 to 1300 years BP as suggested by them. During this prolonged warm, dry period, the "Xerothermic Period" or "Xerothermic Interval" (Sears 1942) or the "Hypsithermal Interval" (Deevey and Flint 1957), it is believed that biota of the Grassland Province shifted eastward through the lower Great Lakes region as far as the Mohawk River valley in New York. Recent studies by Bailey (1972) and Williams (1974) on lakes in northern Indiana do not provide obvious evidence for a massive eastward shift of a large-scale prairie. Perhaps it is best to consider the post-glacial prairie development in northern Indiana, southern Michigan, and western Ohio as an archipelago of small outlying prairies or a mixture of prairie and forest (Sears 1981). Since the classic papers of Gleason and of Transeau, the Prairie Peninsula has remained the subject for extensive discussions including its climate (Borchert 1950), its function as a filter barrier to plant migration (Benninghoff 1964), its invasion by forest elements (Geis and Boggess 1968), its history as inferred from the pollen record (Wright 1968), and the origin and development of the concept itself (Stuckey 1981). A recent summary of the vegetation and climatic conditions of the Prairie Peninsula in Illinois by King (1981) is based on tree pollen diagrams from 3 strategically located bog lakes. His study showed that extensive prairie vegetation replaced deciduous forest about 8300 years BP on the uplands in central Illinois. With a return to increased moisture conditions, renewed forest development occurred about 5000 years BP in the lowlands of southern Illinois.

EXPLANATION AND SOURCES FOR THE DISTRIBUTION MAPS

Information used in developing the plant distribution maps has been obtained from many sources. Major sources of data are maps cited in Phillips and Stuckey (1976), revisions and monographs, state and local floras, atlases of plant distribution maps, state rare and endangered species reports, and herbarium specimens—principally those seen at BH, CU, IND, MICH, MO, NY, NYS, OS, PENN, PH, and US. The wide line in the central states outlines the Prairie Peninsula mapped by Transeau (1935) and the narrow line drawn on selected maps delimits the Atlantic Coastal Plain and/or the Mississippi Embayment. The shaded area is that part of the continent once covered by Wisconsin glaciers. Within and near the Prairie Peninsula, large dots represent specimens collected before 1950 and small dots represent specimens since 1950 (Figs. 2-11 only). This region includes southern Minnesota, southern Wisconsin, southern Michigan, southern Ontario, western New York, western Pennsylvania, Ohio, Indiana, Illinois, Kentucky, Missouri, and Iowa. Elsewhere, all specimen records are mapped with small dots without reference to date. The year 1950 was chosen principally because I expected that the occurrence of any species, if still present within the Prairie Peninsula, would have been documented with herbarium specimens within the past 30 years. Furthermore, the most extensive deterioration of the aquatic and wetland habitats of the Prairie Peninsula has also occurred within the past 30 years.

RELATIONSHIP OF AQUATIC PLANTS TO THE PRAIRIE PENINSULA

Gleason (1923) wrote:

> Ponds were abundant on the Wisconsin drift in Illinois half a century ago, and were notable for the complete lack of such hardy boreal plants as *Comarum palustre* [*Potentilla palustris*] *Dulichium arundinaceum*, and *Menyanthes trifoliata*. They [the ponds] were mostly shallow and easily drained and have long since disappeared. They were also characterized by the absence of deep peat deposits, indicating that they had never been oc-

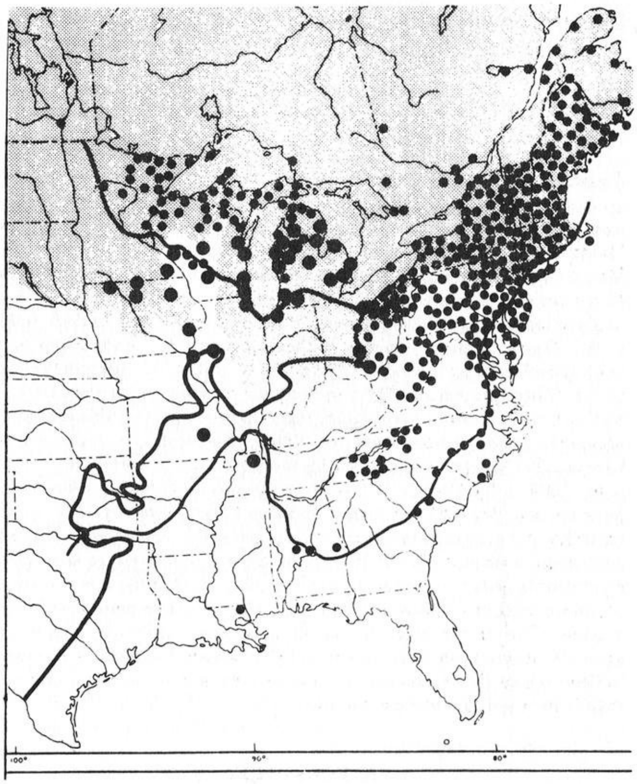

FIG. 2. Map of the distribution of *Potamogeton epihydrus* in eastern North America.

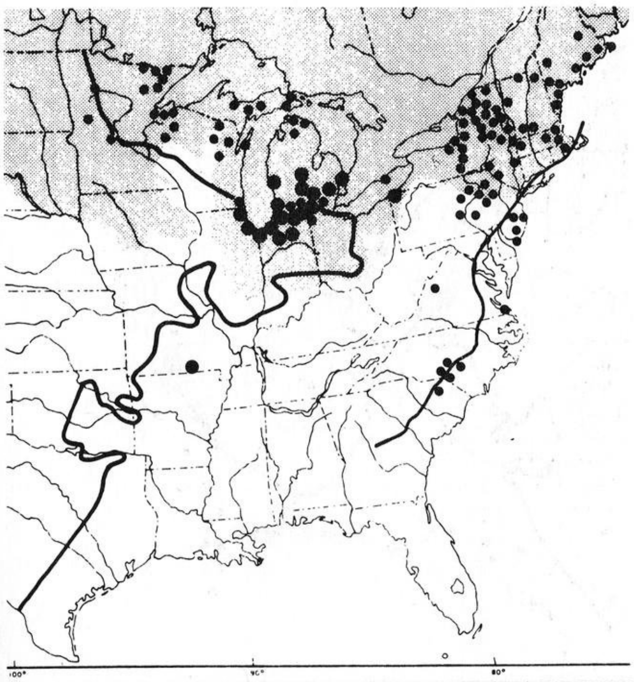

FIG. 3. Map of the distribution of *Scirpus subterminalis* in eastern North America.

> cupied by boreal vegetation and were of comparatively recent origin. . . . This lack of hydrophytic boreal relics toward the southwestern angle of the Wisconsin glaciation is best explained by the assumption of the xerothermic period . . . during which hydrophytic habitats were obliterated toward the west, except in the deepest depressions or local areas affected by subsurface. . . .

It follows from Gleason's statements that certain species of aquatic vascular plants, if once present in the natural wetlands of the Prairie Peninsula, could have since disappeared or become extremely rare during the Xerothermic Period. It should be possible to detect the probable absence of certain species of hydrophytic plants from the Prairie Peninsula by examination of their present-day distribution.

TABLE 1. *p*H values of substrates for 12 aquatic and wetland species rare in or absent from the Prairie Peninsula of North America, as taken from published records on plants occurring in Minnesota, North Carolina, and New England.

SPECIES	MINNESOTA (MOYLE 1945)	NORTH CAROLINA (BEAL 1977)	NEW ENGLAND (HELLQUIST AND CROW 1980, CROW AND HELLQUIST 1981)
Ceratophyllum muricatum (*C. echinatum*)		5.6-6.1	
Decodon verticillatus		5.8-6.7	
Dulichium arundinaceum		5.0-6.6	
Eleocharis equisetoides		5.4	
Eleocharis quadrangulata		6.5-7.3	
Hottonia inflata		6.6-7.1	
Najas gracillima		6.3-8.3	5.7-6.7
Potamogeton epihydrus	6.7-8.6	5.2-7.2	5.0-9.5
Potamogeton pulcher		6.1-6.8	5.6-7.5
Scirpus polyphyllus		6.7-7.4	
Scirpus subterminalis		4.9-6.1	
Sparganium americanum		5.1-6.8	5.3-9.8

Within the past 40 years, dot distribution maps for many aquatic and wetland species of vascular plants have been published individually for the states in or adjacent to the Prairie Peninsula. I have combined these individual maps onto common base maps for correlative and comparative purposes. These new distribution maps have been prepared for over 450 species. The principal references used containing distribution maps are Arkansas (Smith 1978), Illinois (Jones and Fuller 1955; Mohlenbrock 1976; Mohlenbrock and Ladd 1978), Indiana (Deam 1940), Iowa (Beal and Monson 1954; Lammers and Van Der Valk 1977, 1978), Kentucky (Braun 1943), Michigan (Voss 1972), Missouri (Steyermark 1963), Ohio (Braun 1967), Pennsylvania (Wherry, Fogg, and Wahl 1979), Wisconsin (Fassett; Iltis, et al. 1929—), and other areas including the Chicago region (Swink and Wilhelm 1979), the Great Plains (McGregor and Barkley 1977), and southern Ontario (Argus and White 1982). As an example, the distribution of *Sparganium americanum*, as mapped by Beal (1960) and as remapped by combining the data from his map with those maps from recent state floras, has a noticeable gap in the region of the Prairie Peninsula (Fig. 1). Examination of the compiled distribution maps of 21 other species shows similar distributional patterns. The geographical distribution of 12 of these species in eastern North America is shown by dots based on herbarium specimens or on reliable published state maps and plotted on a common base map (Figs. 1-12).

COMMON DISTRIBUTIONAL FEATURES OF THE SPECIES

The distribution patterns of aquatic and wetland vascular plants that are rare in or absent from the Prairie

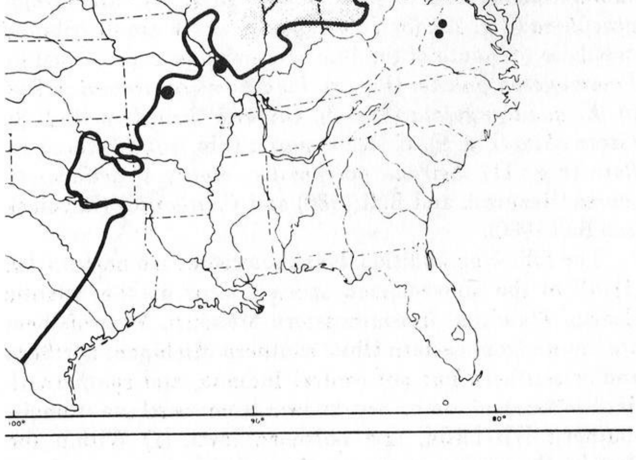

FIG. 4. Map of the distribution of *Scirpus torreyi* in eastern North America.

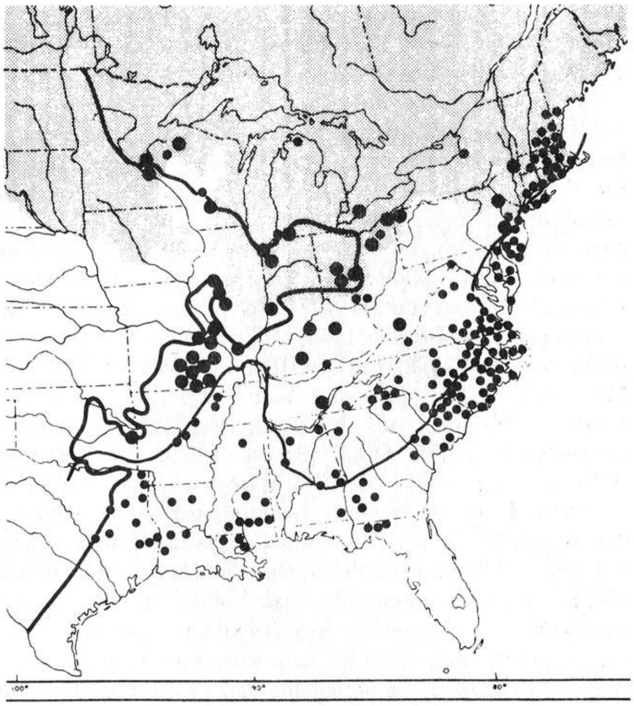

FIG. 5. Map of the distribution of *Potamogeton pulcher* in eastern North America.

Peninsula show certain features in common. The maps reveal that, for the most part, the species occur on the northern to mid-Atlantic Coastal Plain and range into the interior of the continent in the Great Lakes region and/or in the Ohio River valley. Some of them extend southward onto the Gulf Coastal Plain and northward in the Mississippi Embayment reaching westward as far as eastern Texas, eastern Oklahoma, and southeastern Missouri. Three general patterns are evident: (1) Those species which are about equally distributed to the south and north of the Prairie Peninsula, represented by *Sparganium americanum* (Fig. 1), *Decodon verticillatus, Dulichium arundinaceum, Brasenia schreberi,* and *Ceratophyllum muricatum* (*C. echinatum*). (2) Those species which are distributed mostly to the north of the Prairie Peninsula, represented by *Potamogeton epihydrus* (Fig. 2), *Menyanthes trifoliata, Potentilla palustris, Scirpus subterminalis* (Fig. 3), *S. torreyi* (Fig. 4), and *Najas gracillima* (Fig. 12). (3) Those species which are distributed mostly to the south of the Prairie Peninsula, represented by *Potamogeton pulcher* (Fig. 5), *Eleocharis equisetoides* (Fig. 6), *E. quadrangulata* (Fig. 7), *Glyceria acutiflora* (Fig. 8), *Carex alata* (Fig. 9), *C. decomposita* (Fig. 10), *Hottonia inflata* (Fig. 11), *Scirpus polyphyllus, Carex straminea, C. seorsa* (Reznicek and Ball 1980) and *C. atlantica* (Reznicek and Ball 1980).

The following additional characteristics are noteworthy: (1) All of the above-named species occur on the Atlantic Coastal Plain and in southeastern Missouri. Most of them are known from eastern Ohio, southern Michigan, northern and/or southern but not central Indiana, and southern Illinois. Some of them are known from northern Illinois, southern Wisconsin, and northern Iowa. (2) Within the Prairie Peninsula, many of the species have not been documented with specimens since 1950 even though the region is well studied floristically. Of those species which have been determined to be present in the past 30 years, only a very few new localities are known. (3) For the most part, these species occur in soft-water ponds, swamps, and bogs—habitats where the waters are acidic rather than alkaline. Published *p*H values of substrates for 12 of these 22 species reveal that 9 of them are on the acidic side of the

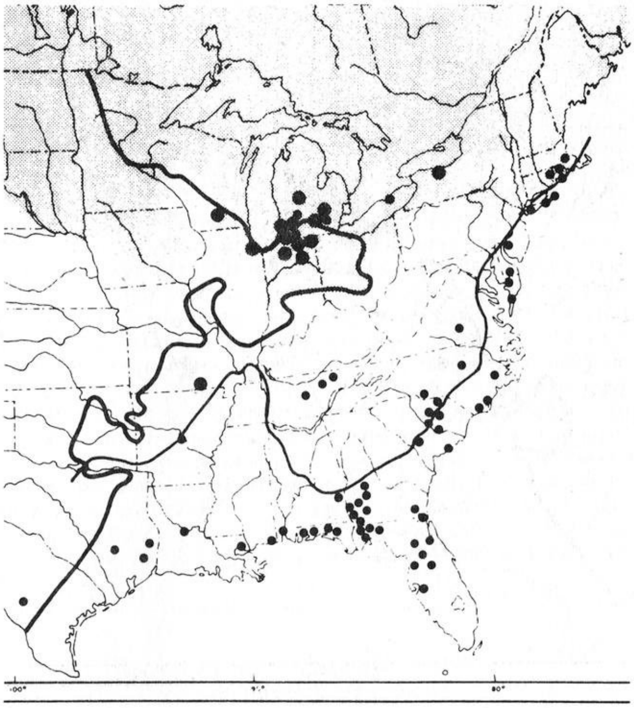

FIG. 6. Map of the distribution of *Eleocharis equisetoides* in eastern North America.

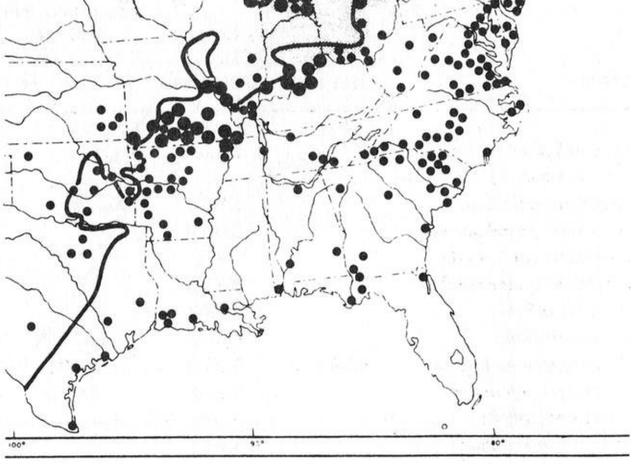

FIG. 7. Map of the distribution of *Eleocharis quadrangulata* in eastern North America.

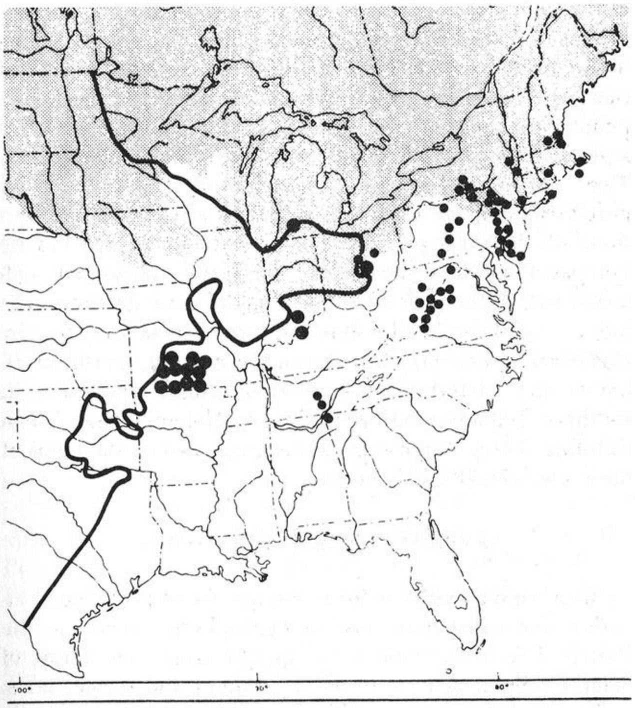

FIG. 8. Map of the distribution of *Glyceria acutiflora* in eastern North America.

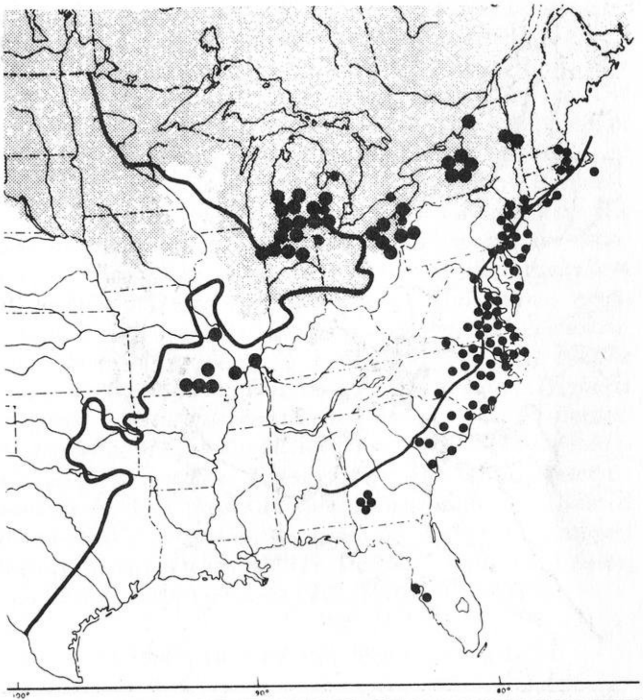

FIG. 9. Map of the distribution of *Carex alata* in eastern North America.

*p*H scale (Table 1). (4) A parallel distribution pattern is also evident among reptiles and amphibians (Conant 1975). Particularly noteworthy examples are shown in the distribution maps of the 5-lined skink (*Eumeces fasciatus*), northern ringneck snake (*Diadophis punctatus*), spotted salamander (*Ambystoma maculatum*), red-backed salamander (*Plethodon cinereus*), four-toed salamander (*Hemidactylium scutatum*), pickerel frog (*Rana palustris*), and wood frog (*Rana sylvatica*).

DISTRIBUTIONAL HISTORY

In an analysis of the flora and vegetation of Missouri, Steyermark (1941, 1949, 1952, 1953, 1963), stated that these Coastal Plain and Mississippi Embayment species inhabit isolated natural, upland sink-hole ponds and swamps in the Ozark Plateau of southeastern Missouri, and are to be considered as among the oldest, if not the oldest, floristic elements of that state. These ponds, resulting from the collapse of the roof of subterranean caverns, occur in the dry, level upland portions of the Ozark Plateau. They also are considered to represent the last remnants of the ancient swampy peneplain that formerly existed in the Ozarks prior to its latest Tertiary uplift. The drainage of these ponds is connected with the underground streams which eventually empty southeastward into the Mississippi River, or southward into the White River drainage, which in turn also drains into the Mississippi. As the Tertiary uplift gradually changed the peneplain from a region of sluggish streams and swampland habitats to the present upland topography with its rocky drier soils and dissected well-drained landscape, the formerly more abundant hydrophytic habitats slowly drained and eventually were reduced to a relatively few localities centered around the present sink-hole ponds. The Xerothermic Period further reduced the occurrence of these strictly aquatic habitats, leading to a decline in the numbers of aquatic and wetland Coastal Plain and Mississippi Embayment species that had survived the Tertiary uplift. Many of these species are also recorded from natural sink-hole ponds in southern Indiana and Kentucky.

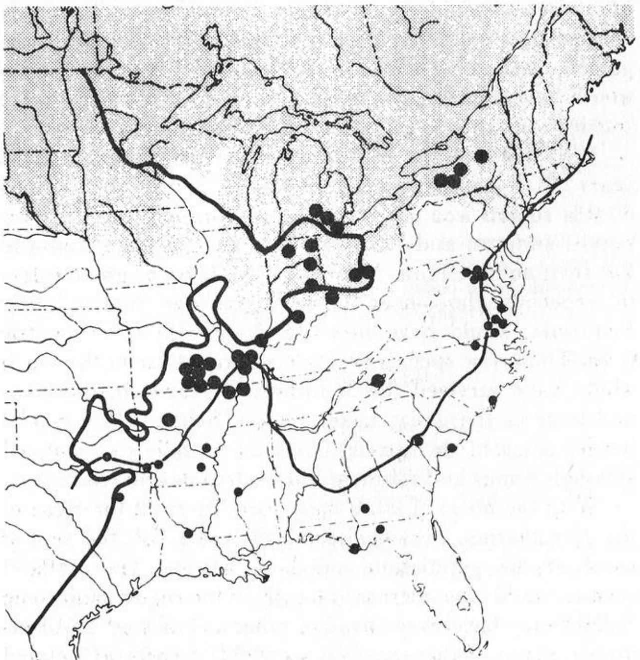

FIG. 10. Map of the distribution of *Carex decomposita* in eastern North America.

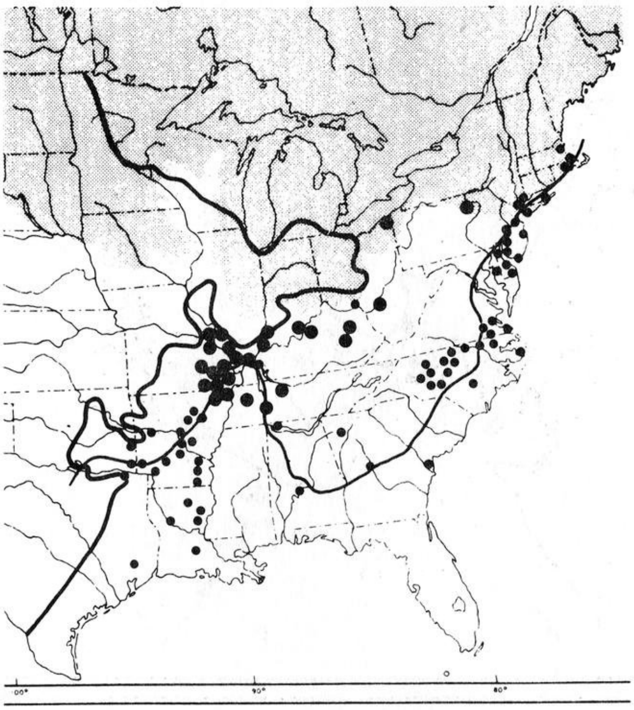

FIG. 11. Map of the distribution of *Hottonia inflata* in eastern North America.

If these species were present at these sites at the end of the Wisconsin, they were readily available for a northward migration immediately following glacial retreat.

With the melting of the ice came the creation of deep kettle lakes, shallow ponds, and meltwater streams and rivers, which provided numerous suitable habitats for colonization by pioneer aquatic and wetland plants in the glaciated territory. A northward migration of these colonizing species would have occurred, and soon the newly created sites would have been occupied with plants. As time passed, assemblages of the hydrophytic vascular plants would have sorted into marshes, swamps, and bogs. Some species undoubtedly migrated farther north than others.

With the onset of the Xerothermic Period, about 8000 years BP, the water levels of the lakes, ponds, and swamps of this region would have dropped considerably. Shallow ponds, swamps, and sloughs would have disappeared and lost their aquatic flora. A few bogs and lakes of greater depth, especially those near the northern edge of the Prairie Peninsula, would have survived along with their aquatic flora. Those few species that had migrated far to the north would have survived the Xerothermic Period in the lakes and bogs of the Great Lakes region. South of the glacial border some of the species survived as relicts in isolated sink-hole ponds and swamps, and in streams and rivers.

With the onset of more mesic conditions at the close of the Xerothermic Period about 5000 years BP, the size of some of the populations of these aquatic and wetland species would have increased locally in the region, and some species may have even invaded other wetland sites. Accordingly, many of these species were still present at isolated sites when European people first settled the Prairie Peninsula. The species were documented at that time, but with the rapid change in use of the land, including draining of the sloughs and swamps for agriculture and increasing use of the ponds and lakes for recreation and industry, the loss of these relict, sensitive species has been pronounced. This loss is evident by the lack of records obtained for most of these species in the past 30 years. Settlement by European people has speeded the process of the disappearance of aquatic and wetland species from the Prairie Peninsula. Two species, *Eleocharis quadrangulata* and *Najas gracillima,* appear to be spreading locally in certain portions of their ranges, but mostly outside of the Prairie Peninsula, as determined from herbarium specimens collected within the past 30 years. This local range expansion into artificially created ponds and reservoirs is occurring by *Eleocharis quadrangulata* in southern Ohio, southern Illinois, and eastern Kansas, and by *Najas gracillima* in southern Indiana, southern Illinois, Alabama, and North Carolina. These range expansions are shown on the maps of these 2 species (Figs. 7 and 12).

EVIDENCE FROM MACROFOSSILS

Confirming evidence for this sequence of post-glacial invasion and subsequent loss of hydrophytic species in the Prairie Peninsula should be sought from the study of macrofossils in peat deposits of remnant and former lakes and bogs of the region. Macrofossil data are increasingly being recorded in connection with palynological studies (Birks 1980), but many more studies from critical localities in the Prairie Peninsula are needed.

The macrofossil record of *Najas gracillima* is an excellent example of the postulated sequence (Fig. 12). The oldest fossils of this species based on radiocarbon dates are from locations south of the glacial boundary and represent populations that lived during the maximum of the Wiscon-

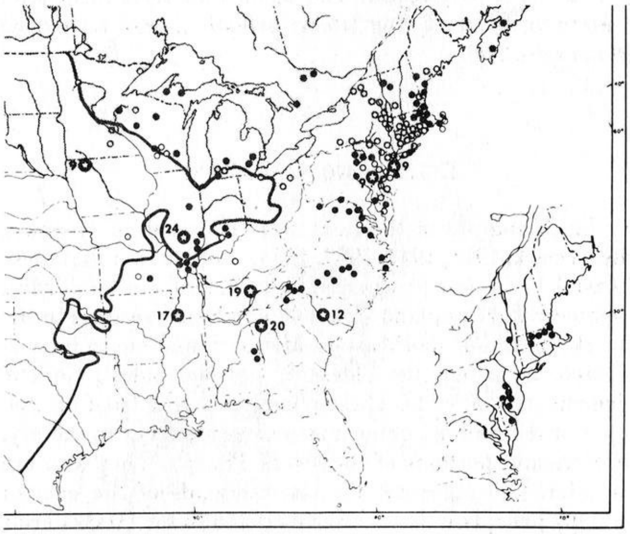

FIG. 12. Map of the distribution of *Najas gracillima* in eastern North America. Circles represent specimen records before 1950 and dots, specimen records since 1950. The herbaria represented are AUA, BH, BOSC, CAN, CU, DAO, F, FSU, GA, GH, IND, KANU, LAF, MICH, MIN, MO, NCSC, NEBC, NY, NYS, OS, PENN, PH, UC, UNA, UNC, UTA, US, VDB, WIS. Large dots with stars in the center represent localities of dated macrofossils, and the number beside the dots is in thousands of years BP. Sources of data are discussed in the text. Small insert map shows the known distribution of non-fossil *N. gracillima* prior to 1900.

sin glaciation. Macrofossil records of *N. gracillima* are mapped (Fig. 12) from Quicksand Pond, Bartow County, Georgia, at about 20,000 years BP (Watts 1970); from Anderson Pond, White County, Tennessee, at about 19,000 years BP (Delcourt 1979); from Nonconnah Creek, Selby County, Tennessee, at about 17,000 years BP (Delcourt et al. 1980); from White Pond, Richland County, South Carolina, at about 12,000 years BP (Watts 1980); from Szabo Pond at about 11,000 years BP and from Helmetta Bog at about 9,000 years BP, Middlesex County, New Jersey (Watts 1979); and from Longswamp, Berks County, Pennsylvania, at about 9,000 years BP (Watts 1979). At Lake West Okoboji, Dickinson County, northwestern Iowa, where *N. gracillima* does not now occur, the fossil fruits of this species are known only from deposits about 9,000 years BP which were preserved since Wisconsinan glaciation but prior to the onset of the Xerothermic Period (Van Zant 1979). This fossil record suggests that *N. gracillima* migrated northward before the formation of the Prairie Peninsula and then disappeared during the Xerothermic Period. The fossils of *N. gracillima* from Pittsburg Basin Lake, Fayette County, Illinois, are from interglacial deposits and hence much older at 24,000 years BP (Grüger) 1972). Confirming evidence for a more diverse aquatic vascular flora in the Prairie Peninsula prior to the onset of the Xerothermic Period would strengthen the hypothesis of the northward migration and subsequent disappearance of many hydrophytic species during the Xerothermic Period.

Additional support may be forthcoming when the macrofossil record is assembled and correlated for other species, including *Brasenia schreberi, Ceratophyllum muricatum, Decodon verticillatus, Dulichium arundinaceum, Menyanthes trifoliata,* and *Potentilla palustris,* plus others not considered in this study, namely *Elatine triandra, E. minima, Eriocaulon septangulare, Hippuris vulgaris, Lobelia dortmanna, Myriophyllum alterniflorum, M. farwellii, M. humile, M. tenellum, Potamogeton robbinsii,* and *P. spirillus.* These latter species are selected because of their presently known distribution and limited macrofossil information as given in recent vegetational history studies (Delcourt 1979, Delcourt, Delcourt, Brister, and Lackey 1980, Van Zant 1979, Watts 1970, 1980).

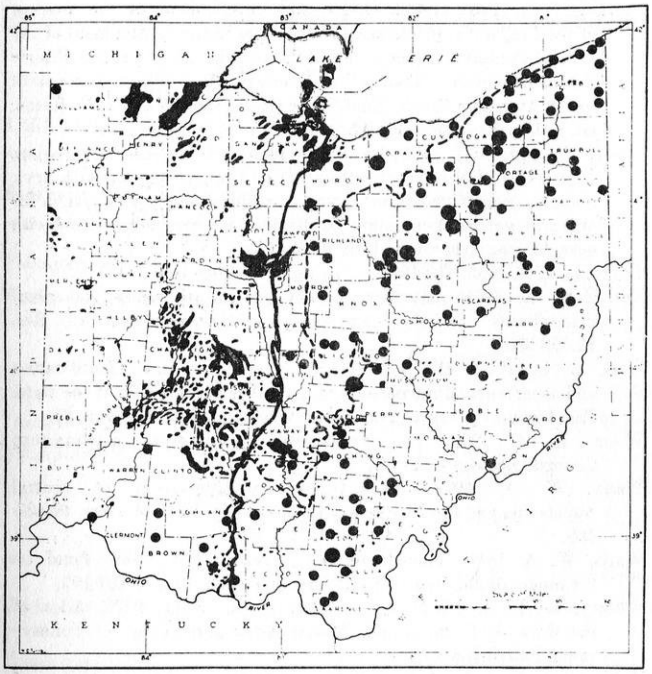

FIG. 13. Map of Ohio showing combined distribution of 16 species mostly absent from the Prairie Peninsula. These species are *Brasenia schreberi, Carex alata, C. decomposita, C. straminea, Ceratophyllum muricatum (C. echinatum), Eleocharis quadrangulata, Glyceria acutiflora, Hottonia inflata, Menyanthes trifoliata, Najas gracillima, Potamogeton epihydrus, P. pulcher, Scirpus polyphyllus, S. subterminalis, S. torreyi,* and *Sparganium americanum.* Shaded areas, primarily in western Ohio, represent prairies as mapped by Transeau in 1950 (Stuckey 1981, map p. 11); the wide north-south line separates the dolomite-limestone bedrock of western Ohio from the shale-sandstone of eastern Ohio; the dashed line depicts the Allegheny Front Escarpment, the western limit of the Allegheny Plateau. Large dots are localities where 4 or more of the 22 species named in this paper have been known to occur (Round Lake, Ashland County; Baumgardner's Pond, Franklin County; Geauga Lake, Geauga County; Jackson Lake, Jackson County; Buckeye Lake, Licking County; Camden Lake, Lorain County; Turkeyfoot Lake, Summit County; Brown's Lake Bog, Donner Lake, and Fox Lake, Wayne County).

DISTRIBUTION OF THE SPECIES IN OHIO

From herbarium specimens, the locations for 16 of the 22 species have been plotted on 1 map for Ohio (Fig. 13). Most of these locations are in the eastern portion of the state, where bedrock is shale or sandstone providing for acidic rather than alkaline hydrophytic conditions. These species also mostly occur east of the Allegheny Front Escarpment in the uplands of the Allegheny (Appalachian) Plateau. Those few localities which share 4 or more of the 22 species are mapped with large dots. These locations are generally natural kettle lakes, relic ponds, or acid bogs, and all of them lie within 30 miles of the Allegheny Front Escarpment. The shaded areas, principally in the western portion of the state, represent the prairie areas as mapped by Transeau (1935). This western region is underlain by calcareous bedrock of dolomite and limestone. When present in the western part of the state, these species occur in those few remnant ponds and lakes with a sustained water supply where they have been able to survive prolonged droughts, and where organic accumulations have formed locally acidic conditions.

ACKNOWLEDGMENTS

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COMPOSITION OF PRAIRIE STANDS IN SOUTHERN MICHIGAN AND ADJOINING AREAS

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Abstract. Prairie plants, 204 species in all, were tabulated for 26 prairie study stands mostly located in southern Michigan.

INTRODUCTION

A number of prairie stands of various types and sizes are scattered through southern Michigan. Although none of these are extensive, quite a few possess considerable diversity. I visited 26 of these sites at different periods of the growing season during the years 1972-81 to observe the composition of the areas (Fig. 1, Table 1). A number of these consist of strip prairies—long, narrow prairie stands extending along railroad rights-of-way. These often exhibit a variety of ecological communities found where conditions range from low, wet habitats along ditches to dry or mesic conditions occurring on higher ground. Some of the stands are fens where slightly alkaline conditions exist.

DISCUSSION OF DATA

The data show that a number of the species are quite rare in this region (Table 2). *Aster sericeus, A. ptarmicoides, Cerastium nutans, Linum sulcatum, Opuntia compressa,* and *Geum triflorum* are found only on dry prairies such as

TABLE 1. List of prairie sites visited.

REFERENCE	SYMBOL	PRAIRIE SITE	COUNTY	LOCATION
Thompson (1975)	A	Algonac St. Park	St. Clair	W of campground, M29 N of Algonac
Thompson (1968)	AA	Ann Arbor	Washtenaw	N of Nichols Arboretum, S bank of Huron River
	Al	Allegan	Allegan	Near 52 St. & 126 Ave., 13 mi. NW of Allegan
	**B	Bowens Mill Fen	Barry	Bowens Mill Rd. at Bassett Lk. Rd., 3 mi. S of Middleville
	**C	Concord Fen	Jackson	Eckert Rd. ¼ mi. of Lippert Rd., 3 mi. S of Concord
Thompson (1978)	**D	Dayton	Berrien	Curran Rd. at McCoy Creek, 2 mi. SE of Dayton
Thompson (1975)	*F	Fairfax RR	St. Joseph	M86 at W edge of Fairfax
	*FB	Fruitbelt RR	Kalamazoo	W of 4 St., N of O Ave., W of Kalamazoo
	G	German Settlers Cemetery	Lake, Ind.	E side of US-41, 1½ mi. S of Cedar Lake, Ind.
	**H	Helmer Brook	Calhoun	NW of Helmer & Harmonia Rds., NW Battle Creek
Thompson (1975)	**I	Indian Bowl	Berrien	E bank of St. Joseph River in Berrien Springs, N of Dean Hill Rd.
Thompson (1975)	J	Jackson RR	Jackson	RR W of Sharp Golf Club, E of Parks Rd., in Jackson
	*K	Klumbis Rd. RR	Cass	RR at Klumbis Rd., betw. Wells & Springs Rds., NE of Pokagon
Bliss & Cox (1964)	L	Lucy Prairie	Lake, Ind.	SE corner of US-41 & US-231, S of St. John, Ind.
	**M	McCoy Fen	Berrien	RR SW of Buchanan at McCoy Creek
Hauser (1953)	N	Newaygo Prairies	Newaygo	Areas near Muskegon River & Oak Rd., 6 mi. E of Newaygo
Thompson (1975)	*O	Otter Creek RR	Monroe	RR betw. S Otter Creek & Cousins Rds., 3 mi S of Monroe
	P	Petersburg	Monroe	Game area on Teal Rd., 2 mi. S of Petersburg
	*PC	Parma-Concord RR	Jackson	RR betw. Parma & Bath Mills Rd.
Walpole (1924)	**R	Riverbank	Washtenaw	Highland Cemetery, River & Holmes Rds., Ypsilanti
Thompson (1975)	*S	West Sturgis RR	St. Joseph	RR 4 mi W of Sturgis at Shimmel Rd.
Walpole (1924)	Sh	Shanghai	Washtenaw	RR & Huron River, 1 mi E of Dixboro Rd., Ann Arbor
Thompson (In press)	SJ	St. Johns	St. Clair	M29 3 mi W of Algonac
	*Th	Thompson RR	Cass	Thompson Rd. at RR, N of White Rd., 1 mi SW of Pokagon
	**T	Teeple Lake Fen	Oakland	Highland Recr. Area NW edge of Teeple Lake
Rogers (1966)	W	Ojibway	Essex	Matchette & Titcombe Rds., S edge of Windsor, Canada

*RR strip prairie stand

**Fen community occupying at least a portion of the site

TABLE 2. Prairie species of stands in southern Michigan and adjoining areas. Key to stands in Table 1. Nomenclature follows Gleason (1952) in some respects.

	Sh	AA	W	L	G	O	PC	FB	Th	K	J	S	F	A	P	Al	N	I	T	C	R	H	M	D	E	SJ
Composites																										
Achillea millefolium	*	*	*	*		*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Antennaria spp.	*	*		*		*	*	*				*	*		*	*	*			*	*	*			*	*
Artemisia caudata																*	*				*					
Aster azureus			*	*	*			*			*		*	*		*	*		*		*					
A. ericoides	*	*	*	*		*				*				*			*		*						*	*
A. faxoni	*		*	*	*										*			*	*				*			*
A. junciformis	*																	*	*	*					*	
A. laevis	*	*	*	*		*	*	*	*		*	*	*	*	*			*	*		*				*	
A. lateriflorus	*	*	*	*							*							*	*	*				*	*	*
A. lucidulus		*					*				*			*				*	*			*	*	*	*	
A. novae-angliae	*	*	*	*	*	*	*	*	*	*	*		*	*	*			*	*	*	*		*	*	*	*
A. pilosus	*	*	*	*	*	*	*	*	*		*	*	*	*	*	*	*	*	*	*			*	*	*	*
A. ptarmicoides																	*									
A. prealtus		*													*			*	*					*	*	
A. puniceus		*												*		*		*	*	*	*		*	*	*	*
A. sagittifolius	*	*	*					*	*		*		*	*		*		*	*		*				*	
A. sericeus																	*									
A. simplex		*				*	*		*		*			*			*	*		*	*		*		*	*
A. umbellatus	*	*	*			*	*				*		*	*	*			*	*	*			*	*	*	
Bidens connata		*				*								*									*	*		*
B. trichosperma									*					*											*	
Cacalia tuberosa																					*		*			
C. atriplicifolia		*				*		*		*				*		*	*				*	*	*			
Chrysanth.leucanthemum	*	*	*	*		*	*	*	*	*	*			*	*	*		*	*	*	*	*		*	*	*
Cirsium discolor	*	*	*	*		*				*	*		*	*	*								*		*	*
																		*	*	*	*	*	*	*	*	*
C. muticum		*	*											*		*										
Coreopsis palmata				*	*			*	*	*		*									*					
C. tripteris	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*					*	*	*	*	*	*	*
Erigeron strigosus	*	*	*	*	*		*	*	*	*	*	*	*	*	*	*	*	*	*		*	*	*	*	*	*
E. altissimum						*																				
E. perfoliatum	*	*	*	*	*	*	*	*	*	*	*	*		*	*	*	*	*	*	*	*		*	*	*	*
Eupatorium maculatum	*	*	*			*	*		*		*		*	*	*			*	*	*	*		*	*	*	*
Helenium autumnale										*				*		*		*							*	*
Helianthus gigantea	*	*	*			*	*		*		*			*				*	*	*			*	*	*	*
H. grosse serrata	*	*	*	*	*	*	*				*			*	*			*	*	*			*	*	*	*
H. maximiliani		*	*			*								*				*								
H. occidentalis	*			*	*		*	*	*			*	*			*	*				*		*		*	
Heliopsis helianthoides		*							*					*				*					*			
Lactuca canadensis	*	*	*	*		*	*	*		*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Liatris aspera	*	*		*		*	*	*						*	*	*	*				*	*	*			
L. cylindracea																*	*								*	
L. novae-angliae	*														*										*	
L. spicata			*	*	*									*		*		*		*	*		*			*

TABLE 2, continued

	Sh	AA	W	L	G	O	FC	FB	Th	K	J	S	F	A	P	Al	N	I	T	C	B	H	M	D	R	SJ
Parthenium integrifolium				*	*																					
Prenanthes racemosa		*	*				*						*	*				*	*	*	*					*
Ratibida pinnata	*	*	*	*	*	*	*	*	*	*	*	*		*							*	*	*		*	
Rudbeckia hirta	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
R. laciniata																					*		*		*	
R. sullivantii																		*					*		*	
Senecio pauperculus	*			*			*			*			*			*	*	*	*	*	*	*	*	*	*	*
Silphium integrifolium				*	*				*	*	*	*						*	*				*	*		
S. laciniatum				*	*																					
S. terebinthinaceum	*	*	*	*	*	*	*	*	*		*			*						*		*	*	*	*	
Solidago altissima	*	*	*	*	*	*	*	*	*	*	*		*	*	*			*	*	*	*		*	*	*	*
S. canadensis	*	*	*	*	*	*	*	*	*	*	*		*	*	*			*	*	*	*		*	*	*	*
S. gigantea	*	*	*	*	*	*	*				*			*	*			*	*	*	*	*	*	*	*	*
S. graminifolia	*	*	*	*	*		*	*	*	*	*			*				*	*	*	*	*	*	*	*	*
S. juncea	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		*	*	*	*
S. nemoralis	*	*	*	*	*	*	*	*	*	*	*		*	*	*	*	*		*		*	*		*	*	*
S. ohioensis														*					*	*		*	*	*	*	*
S. patula																*		*	*		*		*		*	
S. rigida	*	*	*	*	*	*	*	*	*	*	*	*	*	*			*			*	*	*			*	
S. rugosa		*	*				*							*	*			*	*	*	*		*	*	*	
S. riddellii	*	*	*			*					*			*				*	*	*	*		*	*	*	*
S. speciosa	*	*	*	*			*	*	*	*	*			*	*	*	*		*	*	*	*				
S. uliginosa																		*	*	*			*	*		
Vernonia missurica	*	*	*	*		*		*	*		*	*	*	*	*			*	*		*		*	*	*	*
Figworts																										
Castilleja coccinea																		*		*						
Gerardia purpurea						*								*	*			*	*				*		*	*
Pedicularis lanceolata	*	*	*			*					*			*			*	*	*	*			*	*	*	*
Penstemon hirsutum	*		*				*				*				*	*	*			*	*				*	
Veronicastrum virginicum	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		*	*	*		*		*	*	*	*
Grasses																										
Andropogon gerardii	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		*	*	*	*
A. scoparius	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		*		*	*	*		*	
Aristida spp.				*				*							*	*	*		*		*					
Bouteloua curtipendula																									*	
Bromus ciliatus																							*		*	
B. inermis	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		*	*		*		*
Calamagrostis canadensis	*	*	*	*	*	*	*		*		*	*	*	*	*			*	*	*	*		*	*	*	*
Danthonia spicata				*											*	*	*									
Elymus canadensis	*		*	*		*	*	*			*			*	*	*	*	*	*	*			*	*	*	
Hiemchloe odorata			*				*										*			*			*	*	*	
Koeleria cristata																*									*	
Muhlenbergia spp.	*	*		*					*								*	*		*	*		*	*	*	

TABLE 2, continued

	Sh	AA	W	L	G	O	PC	FB	Th	K	J	S	F	A	P	Al	N	I	T	C	B	H	M	D	R	SJ
Panicum implicatum						*					*						*			*					*	*
P. leibergii	*			*						*															*	
P. oligosanthes									*	*							*				*		*			
P. virgatum			*	*	*	*	*		*	*	*		*				*		*				*			*
Sorgastrum nutans	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		*	*	*	*
Spartina pectinata	*	*	*	*	*	*			*		*		*	*		*	*	*	*		*		*	*	*	*
Sporobolus cryptandrus			*							*							*									
S. heterolepis				*																	*					
Stipa spartea					*										*	*	*				*				*	
Legumes																										
Amorpha canescens					*			*				*									*					
Apios americana	*	*	*			*	*		*		*			*	*			*			*		*	*	*	
Baptisia leucantha				*	*		*						*													
B. tinctoria			*	*		*								*	*											
Cassia fasciculata				*																						
Desmodium canadense	*	*	*			*	*		*					*	*		*	*	*		*		*	*	*	
D. illinoense	*	*					*		*			*	*	*					*		*			*		
D. marilandicum	*							*					*								*					
D. sessilifolium																			*							
Lathyrus palustris			*			*								*		*		*	*	*		*	*	*	*	*
Lespedeza capitata	*	*	*	*		*	*	*	*	*	*		*	*	*		*		*	*	*			*	*	
L. hirta								*	*	*				*	*	*	*			*					*	
Lupinus perennis	*						*	*		*		*		*	*	*	*			*	*	*	*			
Melilotus alba	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Petalostemum purpureum				*	*																					
Tephrosia virginiana					*			*								*	*				*	*				
Lilies																										
Aletris farinosa			*				*								*				*	*	*					
Allium cernuum	*	*		*	*				*					*				*		*			*	*	*	
Camassia scilloides				*																						
Lilium michiganense	*	*	*				*					*		*				*	*	*	*	*	*	*	*	
Tofieldia glutinosa																			*	*	*		*		*	
Zygadenus glaucus			*															*		*	*		*		*	
Milkweeds																										
Acerates viridiflora			*													*	*				*					
Apocynum sibiricum		*	*	*		*	*	*	*	*	*	*		*	*	*	*	*	*	*	*	*	*	*		*
Asclepias incarnata	*	*	*			*			*		*							*	*	*	*		*	*		
A. amplexicaulis								*								*										
A. syriaca	*	*	*	*		*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
A. sullivantii			*			*								*												
A. tuberosa	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		*		*	
A. verticillata										*	*	*									*					

TABLE 2, continued

	Sh	AA	W	L	G	O	PC	FB	Th	K	J	S	F	A	P	Al	N	I	T	C	F	H	M	D	R	SJ
Mints																										
Lycopus americanus	*		*			*									*			*	*	*	*			*	*	*
L. uniflorus	*		*																	*	*				*	
Mentha arvensis			*											*	*			*	*					*	*	
Monarda fistulosa	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Pycnanthemum virginianum	*	*	*	*	*	*	*		*		*	*		*	*			*	*	*	*	*	*	*	*	*
Roses																										
Filipendula rubra																		*				*				
Fragaria virginiana	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Geum triflorum																	*									
Potentilla arguta			*								*					*	*									
P. canadensis	*		*	*	*	*	*	*	*	*	*			*	*	*	*	*	*	*	*	*	*	*	*	
P. fruticosa																			*	*	*	*	*		*	
Crowfoots																										
Anemone canadensis	*	*	*			*	*		*		*			*		*	*		*	*	*			*	*	
A. cylindrica	*								*	*		*	*	*	*		*		*		*			*		
A. virginiana	*	*	*				*		*		*				*		*			*	*		*	*		
Caltha palustris		*					*						*		*				*	*		*	*	*	*	
Ranunculus fascicularis															*	*					*					
Thalictrum dasycarpum	*	*	*			*	*		*	*	*	*		*			*	*	*	*	*	*	*	*	*	
Rushes																										
Juncus dudleyi			*								*															
J. greenei																	*				*					
Umbels																										
Angelica atropurpurea		*					*		*									*		*		*	*	*		
Daucus carota	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Eryngium yuccifolium				*	*				*			*											*			
Oxypolis rigidior		*	*	*			*				*			*				*		*	*	*	*	*	*	
Zizia aurea	*	*		*	*	*	*	*	*	*	*	*			*			*		*	*	*	*	*	*	*
Shrubs																										
Ceanothus americana	*		*	*				*	*	*						*					*		*	*	*	
Celastrus scandens	*	*	*														*									*
Corylus americana			*				*	*	*	*							*		*	*	*	*	*	*	*	
Rhus copallina			*				*				*				*	*										
R. glabra	*	*	*	*			*				*														*	*
Rubus flagellaris	*	*		*	*		*	*	*	*	*				*	*			*	*	*	*	*	*		
Salix humilis	*	*	*	*		*	*	*	*	*					*						*	*	*		*	
Other species																										
Equisetum arvense	*	*	*			*	*											*		*		*	*	*	*	
E. laevigatum							*								*			*		*		*	*	*	*	
Onoclea sensibilis	*					*	*		*		*	*			*	*		*	*	*	*	*	*	*	*	
Thelypteris palustris	*	*	*			*	*		*		*				*	*		*	*	*	*	*	*	*	*	*
Tradescantia ohiensis			*	*	*	*	*	*	*	*	*	*		*		*	*	*		*	*	*	*	*	*	
Hypoxis hirsuta			*	*		*	*				*			*	*			*		*	*	*	*	*	*	*

TABLE 2, continued

	Sh	AA	W	L	G	O	PC	FB	Th	K	J	S	F	A	P	Al	N	I	T	C	B	H	M	D	R	SJ
Iris shrevei	*	*	*	*		*	*	*						*	*	*		*	*	*		*	*	*	*	*
Sisyrinchium albidum	*			*	*	*	*		*	*	*	*						*	*	*	*	*	*	*	*	
Cypripedium calceolus	*																					*				*
C. candidum																		*		*			*	*		*
Habenaria lacera						*															*					
Spiranthes cernua	*					*						*		*	*			*	*		*		*			*
S. romanzoffiana																		*							*	
Comandra richardsiana	*		*	*	*		*	*	*	*		*	*		*	*	*	*		*	*	*	*	*	*	*
Arenaria stricta																*										
Cerastium nutans																	*									
Stellaria longifolia											*							*							*	
Heuchera richardsonii	*			*	*	*	*		*		*	*		*			*	*		*		*			*	
Parnassus glauca	*	*												*				*	*	*	*		*	*	*	
Saxifraga pensylvanica		*		*			*		*							*	*	*		*		*	*	*	*	
Linum sulcatum																*	*									
Polygala senega																		*			*				*	
Euphorbia corollata	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		*	
Helianthemum canadense	*	*				*							*	*		*	*	*			*				*	
Viola cucullata																*		*							*	
V. pedata-pedatifida									*							*	*				*					
V. sagittata				*									*			*	*				*					
Opuntia compressa																*	*									
Lythrum alatum		*	*			*					*			*				*	*			*				*
Oenothera biennis	*	*	*			*		*		*			*	*	*	*	*	*	*		*		*	*	*	*
Gaura biennis			*			*					*															
Dodecatheon meadia				*	*																		*	*		
Steironema quadriflorum	*	*	*											*	*	*	*	*	*	*	*			*	*	*
Gentiana alba	*								*	*																
G. andrewsii			*			*			*		*			*	*			*			*		*	*		*
G. crinita-procera			*								*							*		*	*		*		*	
G. puberula				*																						
Swertia caroliniensis										*						*		*								
Phlox maculata																							*	*		
P. pilosa		*	*	*	*		*				*	*		*						*	*	*			*	
Polemonium reptans																		*				*	*			
Lithospermum canes.-caro.	*		*	*	*				*	*		*	*			*	*			*	*	*			*	
Galium boreale	*	*	*	*			*		*	*				*					*	*	*	*	*	*	*	*
Valeriana ciliata																		*	*	*	*	*	*	*	*	
V. septentrioalis																									*	
Campanula aparinoides	*	*																*	*	*			*		*	
Lobelia kalmii																		*	*	*	*		*	*	*	
L. siphilitica																*		*	*	*	*		*	*	*	
L. spicata	*		*	*		*								*	*	*	*		*		*					*

Newaygo and Allegan. *Camassia scilloides, Cassia fasciculata,* and *Gentiana puberula* were observed only at Lucy Prairie, which is situated at the southwest edge of the study region. *Silphium laciniatum* and *Petalostemum purpureum* occur only at this location and at German Settlers cemetery. *Dodecatheon meadia* provides a showy display at both of these sites but is only of limited occurrence at McCoy and Dayton fens. *Cacalia tuberosa* is found at McCoy and Bowens Mill sites, whereas *Filipendula rubra* occurs only at Helmer Brook and Indian Bowl. *Phlox maculata* is a rare species limited to Dayton and McCoy fens.

Species conspicuous in fens include *Lobelia kalmii, Cypripedium candidum, Potentilla fruticosa, Gentiana crinita* or *procera, Valeriana edulis* var. *ciliata,* and *Zygadenus glaucus.* Other species are *Lobelia siphilitica, Castilleja coccinea, Tofieldia glutinosa, Polemonium reptans,* and *Solidago patula.*

Data suggest that *Asclepias sullivantii, Sanguisorba canadensis,* and *Gaura biennis* are confined to the eastern portion of the region, where *Amorpha canescens, Asclepias amplexicaulis, Tephrosia virginiana, Eryngium yuccifolium, Dodecatheon meadia,* and *Polemonium reptans* are largely limited to the western section of the study area.

It is evident that a number of species are common on most of the prairie sites. As a group, asters and goldenrods occur quite frequently on prairies. Most of the other members of the composites listed fall in the same category except for a few rarer species such as *Parthenium integrifolium, Liatris novae-angliae,* and *Eupatorium altissimum.* Common species in other families include *Fragaria virginiana, Potentilla canadensis, Thalictrum dasycarpum, Desmodium canadense, Lespedeza hirta* and *L. capitata, Melilotus alba, Zizia aurea, Monarda fistulosa, Pycnanthemum virginianum,* and *Euphorbia corollata.* Also, widespread are *Daucus carota, Onoclea sensibilis, Thelypteris palustris, Tradescantia ohiensis, Sisyrinchium albidum, Comandra umbellata* var. *decumbens, Oenothera biennis, Lithospermum canescens, Galium boreale, Apocynum sibiricum, Asclepias syriaca,* and *A. tuberosa.* Still other frequent species are *Veronicastrum virginicum, Andropogon gerardii, A. scoparius, Bromus inermis, Calamagrostis canadensis, Elymus canadensis, Panicum virgatum, Spartina pectinata, Sorghastrum nutans, Rubus flagellaris,* and *Salix humilis.*

The largest group represented on the various prairie sites is the composite family; the next largest group is the grass, and the third largest, the legume family.

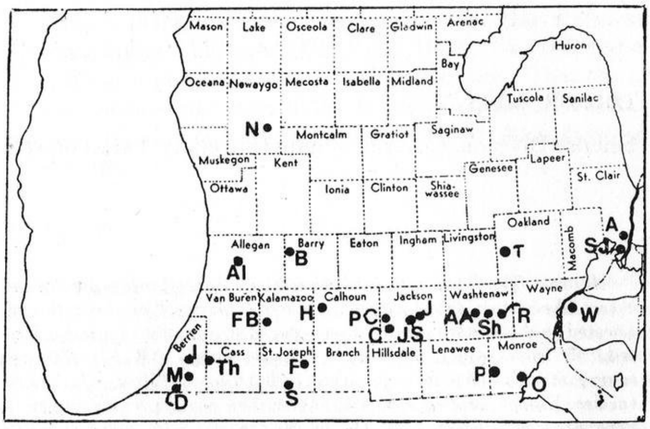

FIG. 1. Location of prairie stands in southern Michigan. Symbols listed in Table 1.

ACKNOWLEDGMENTS

Most of the species list was based on field data I collected from surveys of the different prairie sites. However, a few missing species were added by other investigators. I wish to thank the following for this material: Heidi Appel, Kim Chapman, Margaret Kohring, Ronald Kapp, Max Medley, Daniel Nepstad, Robert Pleznac, Edward Scharrer, and Leon Schaddelee. I thank Cranbrook Institute of Science for research funds.

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THE CHICAGO RIDGE PRAIRIE — A FLORAL SUMMARY

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Abstract. The Chicago Ridge Prairie (Cook County) represents the last extant lake-bottom, gravel-outwash, calcareous black-soil prairie in Illinois. Located on the western plain of a post-glacial stream, this prairie has been reduced from several hundred to approximately 3.8 ha. Although somewhat disturbed at its edges, it still (1981) has over 150 vascular prairie species. Except for *Poa* spp., the undisturbed portion of the prairie is generally free of weedy taxa. The prairie features a low ridge-and-swale topography, with 2 major textures, silty clay loams and silt loams, plus spots of muck. This topography and soil, underlain by stony, gravelly outwash, creates an undulating pattern of 3 main prairie associations—wet-mesic, mesic, and dry-mesic—compressed into a relatively small area. Soils are alkaline, with a *p*H range of 7.8 to 8.5. Certain calciphile species are present here, while apparently absent in the surrounding black soil mesic prairies. In the wettest areas, a *Carex-Senecio-Calamagrostis* association exists. In the more mesic sections, the prairie is dominated by a *Silphium-Andropogon-Liatris* association, while the driest portions contain an association dominated by *Sporobolus heterolepis*. Typical leguminous species are absent here, but recorded in nearby prairies indicating a depauperate situation for this family. The Natural Area Rating Index for this prairie is 73, among the top natural prairie areas in the areas in the state. A history of spring and fall prairie fires exists for this site. Today, nearby construction activities threaten the destruction of this privately owned, forb-rich, high quality tallgrass prairie.

INTRODUCTION

At the completion of the Illinois Natural Areas Inventory, 391 acres of Class A and B tallgrass prairie were identified as remaining in Cook County (White 1978). Cook County ranked second in prairie acreage statewide (White 1978: 176). Many of these natural areas remain threatened by changes in land-use patterns. One is an unprotected wet-mesic/mesic black-soil prairie commonly known as the "Chicago Ridge Prairie," located approximately 24 k (15 miles) southwest of downtown Chicago (SW¼, NE¼, Sec. 17, T37N, R13E, Worth Township). The site is in private ownership.

The prairie is bounded on the north by 105th Street, on the east by Menard Street (extended) and on the south and west by the Chessie/IBH railroad (RR) tracks; it is triangular in shape (Fig. 1).

What remains of the Chicago Ridge Prairie (CRP) study site covers 5.17 ha (12.83 acres), although as recently as 1978 it covered 11.7 ha (29 acres). In 1979 construction of an apartment complex destroyed the eastern 6.85 ha (17 acres). Debris from that project filled about 1.4 ha (3.5 acres) of the current study site, reducing the area in prairie vegetation to about 3.76 ha (9.04 acres). A study of the tract records for the current parcel indicates it was owned by the federal government from 1839 to 1916 and has remained in a private trust most of the time since. There is no evidence of any past systematic development or agricultural use of the land, including plowing. However, nearby residential construction activities have disturbed the site in the last 10 years. The prairie represents virtually the last high-quality remnant of mesic black-soil prairies in Worth Township.

The CRP is unusual, however, in that it is moderately calcareous, with soils based on gravel outwash and in that it contains the locally endangered white lady-slipper orchid (*Cypripedium candidum*) in a prairie community rather than fen community where populations are now typically found.

The objectives of this study were twofold: (1) to inventory flora of the site prior to further disturbance or destruction and (2) to note the environmental conditions under which this flora exists.

ENVIRONMENTAL FEATURES

The CRP is found within the Northeast Morainal Division, Chicago Lake Plain Section, 1 of the natural divisions of environments and communities in the state (Illinois Nature Preserves Commission *in* Mohlenbrock 1975). This remnant is located on a portion of the old outwash bed of a post-glacial stream, which formed part of the Sag outlet, a glacial water sluiceway, during the Tolleston beach stage of glacial Lake Chicago (Schneider and Keller 1970, Linebach 1979, Bretz 1939). The site is just northeast of the Calumet stage beach of Worth Island. The CRP is within 0.3 km (0.18 mile) of modern Stony Creek, which delineates the Pleistocene drainageway into the Calumet-Sag Channel

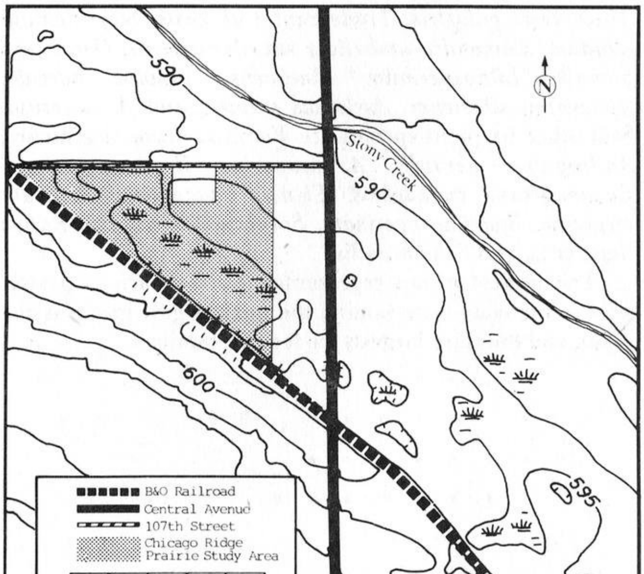

FIG. 1. Part of the Palos Park (Ill.) quadrangle map showing the location of the Chicago Ridge Prairie and area near the post-glacial stream, Stony Creek. Note that the prairie is located on the outwash plain of that stream.

(Willman 1971). The CRP site is probably a terrace remnant of the valley train flush that deposited stony, gravelly material here and covered it with an alluvium of silt, muck and clay (Schneider and Keller 1970). These events were apparently localized and restricted to this relatively narrow corridor, resulting in calcareous sorted deposits different from the sandy and clayey lacustrine sediments which underlie much of the soils of nearby Oak Lawn (Mapes 1979). The soils (such as Drummer, Mundelein, and Barrington) which developed along the southern side of Stony Creek are developed on outwash and terrace deposits (Mapes 1979). As a result of these deposits, the soils at CRP are moderately alkaline. In addition, the topographic position of the Mundelein ridge contributes to a swell-and-swale drainage pattern within a relatively small range of altitude. (See U.S.G.S. 7½-minute topographic map, Palos Park quadrangle, 1963). The relief does not exceed a difference of 1.4 m (4.7 ft.).

The 2 soil series at CRP are Peotone (332) and Mundelein (442), which comprise about 70% and 30% of the total land area, respectively. They belong to the Drummer-Mundelein-Barrington Association. Almost all the cut-and-fill area (about 1.4 ha) occurs within the Peotone soil. Peotone soils are described (Mapes 1979) as silty clay loams and Mundelein soils as silty loams, both poorly drained, but the former more so. Inclusions of Houghton muck and stony deposits occur within these soils. In addition, soil-water capacity and organic content of these soils are described as high. Indeed, observations at CRP since 1975 indicate standing water, especially in the Peotone soil, during spring and occasionally in the summer after heavy rains. Since 1979, however, a noticeable (but not measured) decline in ponding has occurred, apparently due to drainage changes attributable to development of the eastern portion of the 1978 prairie (described above).

During the 1925 U.S.G.S. land survey and in the 1963 aerial revision, the 11.7-ha area was mapped, in part, as marsh/wetlands, between 590 feet and 595 feet above sea level (Stony Creek is about 585 feet above datum). The area between 595 feet and 600 feet, mostly the western and northern portions of this triangular parcel, are mapped as dry. Apparently the back side of the Mundelein terrace-ridge partially impeded water flow, maintaining a high water table, a characteristic condition of the post-glacial sluiceway topography (Willman 1971, Bretz 1939). The RR embankment also physically restricts the water flow. That the area was once wetter than today is indicated by area soil and topographic maps and local tales of past duck hunting at the site.

TABLE 1. Leading plant families represented in the flora of the Chicago Ridge Prairie (based on Appendix).

Family	No. of genera	No. of species	% of total species
Compositae	21	49	31.8
Gramineae	14	16	10.4
Labiatae	09	10	6.5
Cyperaeae	03	08	5.2
Leguminosae	05	06	3.9
Asclepiadaceae	01	06	3.9
Scrophulariaceae	04	05	3.2
Liliaceae	03	05	3.2
Umbelliferae	04	04	2.6
Totals	64	110	70.7
All taxa total	98	154	98.9

Methods

Floristic observations of the then 11.7-ha (29-acre) prairie, initiated in 1975 plus consultation with area naturalists on the taxa present resulted in a preliminary species list at the end of 1978. Field studies of the site continued through 1982, resulting in the flora summarized in the Appendix. When part of the prairie was destroyed in 1978, the remaining area was rechecked for extant species. Initially, voucher specimens were not taken because of the small size of the tract, disturbance concerns, and small population size of some taxa. In 1981 and 1982, voucher specimens of selected species were taken and placed in the herbarium of Governors State University. The identification of the collected material was made with Swink and Wilhelm (1979) and Mohlenbrock (1975). Nomenclature follows usage of Swink and Wilhelm (1979), except for *Castilleja coccinea* forma *lutescens* and *Heuchera richardsonii grayana* where Mohlenbrock (1975) is followed. In 1981 and 1982, selected environmental features were studied, including soils and topographic relief, and mapped. Soil study methods were adopted from Cox (1980) and Hesse (1971).

Results And Discussion

Floristic observations on the prairies of the Chicago region have been made since the 1880s, as the presettlement Chicago area was botanically rich (Higley and Raddin 1891). Prairie inventories are described in reports by Vestal (1914) for an Elmhurst prairie, Paintin (1929), Betz and Cole (1969), and later Apfelbaum and Rouffa (1981) for the Peacock Prairie.

The best overall description of Chicago prairie community types is found in Betz (1965). The most thorough reference published on prairie species associations for the Chicago area is Swink and Wilhelm (1979). With the destruction of most prairie areas in the Chicago area, new knowledge of Chicago area prairies will be scarce. This report summarizes the flora for the last known lake bottom, calcareous prairie developed on soils derived from glacial outwash in Illinois.

The Flora

A total of 154 species (not including exotic and woody plants) has been reported as part of the plant community of the CRP through the growing season of 1981 (Appendix). Although 38 families and 98 genera are represented, more than 50% of the species (89) are found in 5 families (Compositae, Gramineae, Labiatae, Cyperaceae, and Leguminosae) and 52 genera. Data on taxa representation in the 9 leading families is given in Table 1. With the exception of the Cyperaceae, Curtis (1959) found the same leading families in similar inter-family ratios for mesic and wet prairies (there are nevertheless important differences between Illinois and Wisconsin prairie community types).

Earlier unpublished floristic studies of the Chicago Ridge/Oak Lawn area surrounding the CRP indicate the presence of 23 species not currently found at the CRP (Table 2). Inasmuch as these Worth Township prairies also occurred on level or gently undulating glacial lake bottom

TABLE 2. Prairie species not currently reported at Chicago Ridge but formerly present in the nearby Oak Lawn area black soil prairie remnants (now destroyed) as reported by Marion Cole and David Blenz (1967, personal communication) and author. Nomenclature follows Swink and Wilhelm (1979).

SPECIES
Asclepias incarnata
Aster ×lutescens
A. sericeus
Baptisia australis
B. leucantha
B. leucophaea
Carex bicknellii
Claytonia virginica
Gentiana puberula
Helianthus laetiflorus rigidus
Hierochloe odorata
Houstonia caerulea
Liatris cylindracea
Panicum oligosanthes scribnerianum
Pedicularis canadensis
Petalostemum candidum
Polygala sanguinea
Potentilla arguta
Rudbeckia subtomentosa
Salix humilis
Solidago missouriensis fasciculata
Viola sagittata
V. sororia

topography as contiguous areas with each other, the absence of these species from the CRP poses an interesting problem. Spot samples of soil from the Oak Lawn prairie indicate a higher sand content and lower *p*H (≤ 7). At the CRP, soil *p*H for the Peotone and Mundelein soils ranged from 7.8 to 8.5, moderately calcareous. Calciphile species present at CRP are notably absent from the flora of Oak Lawn (e.g. *Valeriana ciliata, Aster ptarmicoides, Satureja arkansana*). While soil *p*H preferences might explain the distribution of a calciphile species, it does not account for the absence of such leguminous species as *Baptisia* spp., *Vicia americana*, and *Psoralea tenuiflora*. Somewhat sandy soils in Oak Lawn may account for the presence of *Aster sericeus, Cassia fasciculata*, and *Houstonia caerulea*. The unavailability of complete floras for nearby prairies makes it difficult to compute indices of similarity. Although there are noteworthy differences between these prairies, presence values for most of these prairie species would be high. Presence alone, however, does not indicate density or frequency of occurrence, which might vary widely as each prairie community is closely adjusted to local environmental conditions in both composition and diversity.

Plant Associations

The plant associations in the CRP are distributed along soil moisture gradients (microgradients) developed, in part, in response to small topographic relief changes (microrelief), ranging to about ± 0.70 m (2.4 feet). Ordinarily such micro-relief is not indicated on most maps and may not be visible to the untrained observer. Nevertheless, the flora of the CRP is distinctly patterned according to the microrelief, thus suggesting the existence of a relatively sensitive correlation between vegetation and contour—a coenocline. Glenn-Lewin and Crist (1981) found that species distribution was related to flooding events, as determined by elevation, in an Iowa prairie pothole. Where the elevational change is abrupt, the boundaries of the association are more pronounced. In areas where the changes are gradual, the associations grade into each other. (Only 1 woody species [*Populus deltoides*] occurs; weedy taxa are restricted to roadsides and construction disturbances.)

Today the flora comprises 3 major prairie associations: (1) wet-mesic, originally the largest type; (2) mesic; and (3) dry-mesic. This natural community would be recognized as a "mesic prairie" using the classification scheme White (1978) developed for Illinois natural communities. For this study the soil moisture classes of White (1978) were adopted. This drainage catena generally follows the concept of Curtis (1959), although its expression at CRP has been complicated by recent area changes and urbanization and sewer installation along the periphery of the prairie. In addition to these hydrological disturbances, the prairie has a history of natural spring and/or fall burns for the last 3 years and irregularly prior to 1978. Apparently the recent lowering of the water table has encouraged more frequent and thorough burns. In response to these factors, the ratio of these plant associations to each other has probably shifted towards more mesic conditions.

To compare prairies along a moisture gradient, Curtis (1959) described a prairie continuum with 5 moisture classes from wet to dry. His approach was applied to the CRP and 3 other black-soil Cook County prairies (Table 3). All the computed indices fell within Curtis' range of wet-mesic to mesic. However, using White's soil moisture class descriptions, based on today's hydrology, the CRP would range from wet-mesic to mesic to dry-mesic.

The Wet-mesic Association. This association was the dominant association of the original 11.7-ha prairie and continues today as the major association. While the wet-mesic association is found in both Peotone and Mundelein mapped soils, it is more widespread in the former. In the lowest swales, the soils tend to be mucky and the species diversity low. Generally the wet-mesic habitats occur at an elevation below 595 feet above sea level and occupy the areas on either side of the outwash terrace ridge (generally above 595 feet above datum). Formerly, some of these areas contained standing water during spring and summer, but now, due to improved drainage, water is restricted to early spring. These habitats contain elements of wet prairie.

TABLE 3. Moisture gradient indices for selected Cook County, Illinois prairies based on indicator species of Curtis (1959).

PRAIRIE (STUDY YEAR)	INDEX VALUE*	MOISTURE GRADIENT
Chicago Ridge (1981)	257.5	Wet Mesic/Mesic
Chicago Ridge/Oak Lawn (1967)	199.8	Wet Mesic
Peacock Prairie (1981)	266.7	Wet Mesic/Mesic
Oak Lawn Prairie (1975)	245.5	Wet Mesic

* Possible Range = 100 (wet) - 500 (dry)

Species usually associated with wet prairie (e.g. *Calamagrostis, Carex, Iris*) are common in certain sections, though their habitat would now be classified as wet-mesic.

The wet-mesic dominants form the *Carex-Senecio-Calamagrostis* association. Extensive stands of *Carex stricta* and *C. buxatumii* are conspicuous throughout this habitat. *Calamagrostis canadensis* is intermixed with *Carex*, primarily in the upper portion of the wet-mesic microgradient. Prominent in the early spring aspect here are the basal leaves of 2 species of *Senecio* which form a widespread ground cover. In some swale areas, circular patches of *Senecio* seem to exclude other species. In some of these areas only a few *Spartina, Viola*, and *Valeriana* were observed. These species were surrounded by *Carex, Stachys*, and scattered individuals of *Silphium laciniatum*. In most of the swales, *Senecio aureus semicordatus* is more common than *S. pauperculus balsamitae*. Swink and Wilhelm (1979) note that *S. pauperculus* occurs in sedge meadows and moist prairies, elements of which all overlap at CRP. The late spring flowers of *Senecio*, at or just below the growth level of the grasses and sedges, provide a striking yellow display. The lowest spots are filled with dense patches of *Iris virginica shrevei*.

As summer progresses, the number of flowering forbs increases. Common plants, in addition to the dominants, are *Phlox glaberrima interior, Equisetum arvense, Lycopus americanus*, and *Veronicastrum virginicum*, the last appearing colonial. Frequent at the edges of the swales are *Allium cernuum, Spartina pectinata, Physostegia virginiana, Silphium laciniatum*, and *Valeriana ciliata*. Conspicuous but less frequent are *Apocynum sibricum, Cicuta maculata, Convolvulus sepium, Cacalia tuberosa, Lysimachia quadriflora, Galium obtusum, Teucrium canadense, Stachys tenufolia hispida, Coreopsis tripteris, Verbena hastata, Vernonia fasciculata*, and *Helenium autumnale*. Rare are *Asceplias sullivantii, Dodecatheon meadia* and *Eupatorium perfoliatum*. The transition zone to mesic conditions is marked by intermixed stands of *Calamagrostis canadensis, Panicum virgatum*, and *Andropogon gerardii*.

Except for the conspicuous *Senecio* openings, the forbs, grasses, and sedges provide a dense cover over 1 m tall, in contrast to the remainder of the CRP where the grass density is lower.

The Mesic Association. This association is located on the better-drained sections of both Peotone and Mundelein mapped soils, upslope from the wet-mesic area on the microgradient. Mesic prairie is located in the northeastern, southwestern, and northwestern sections of the prairie. A number of linear "islands" and small mounds, approximately 0.5 m (1.6 feet) above the surrounding land are scattered throughout the prairie. These islands and mounds apparently provide habitat for voles, ground squirrels, and mice, while serving as sites for more fugitive prairie plant species (e.g., *Coreopsis tripteris, Eryngium yuccifolium*, and *Silphium terebinthinaceum*). The mesic sites are interrupted by wet-mesic swales, but these are patches rather than contiguous strips—a swell-and-swale microtopography. Each main mesic area has experienced some type of disturbance—the most disturbed lying in the northeastern corner of the CRP. Systematic removal of the top 15 cm of soil is evident in a portion of the lower southeastern section now covered with railroad cinders. This disturbance appears to have occurred over 50 years ago. The area is completely revegetated by only mesic prairie species.

The mesic association has the highest species diversity. It includes a majority of the calciphile species occurring at CRP (about 15% of the species in the Appendix demonstrate affinities for calcareous habitats according to Swink and Wilhelm [1979]). In all the mesic areas, *Silphium terebinthinaceum, Andropogon gerardii*, and *Liatris spicata* form the dominant association, although they vary widely in their density. The somewhat disturbed northeastern mesic corner contains an abundance of *Liatris spicata*, with *Poa pratensis* serving as the disturbance indicator. In this section *Andropogon scoparius* is found with small clumps of the other prairie grasses but *Poa* predominates. The *Desmodium* and *Anemone* are found here. *Satureja arkansana* and *Scutellaria parvula* flourish here as well as *Asclepias verticillata*, possibly as a result of reduced tallgrass competition due to past disturbances.

The medium-moist section north-centrally located near 105th Street contains most of the mesic species. Surprisingly, a rather large population of the rare and locally endangered (White 1978) small white lady-slipper orchid *(Cypripedium candidum)* occurs in association with *Zizia aurea* as noted by Swink and Wilhelm (1979). The orchid, 1 of 2 orchids in the prairie, has been observed in bloom as early as 5 May. Three color forms of the Indian paint brush (*Castilleja coccinea*) occur in a massive spring display. These displays are augmented by numerous bloomings of *Lithospermum canescens, Sisyrinchium albidum, Dodecatheon meadia*, and *Phlox pilosa*. While *Valeriana ciliata* is found throughout most sections of the prairie, it is most concentrated on the mesic rise on the western and southern edges of the wet swales; it is one of the first plants to bloom in spring and provides dominance at that time.

The summer and fall aspects of these mesic sections are typical for black soil prairies in the Chicago area such as Peacock Prairie (Paintin 1929). *Petalostemum purpureum, Aster ptarmicoides*, and *Physostegia verginiana* are especially abundant. Common in the late summer are *Liatris aspera, Aster azureus, Solidago riddellii*, and *Gentiana quinquefolia*, which extend into the dry-mesic plateau. A rather rare mesic species is *Cirsium hillii* which is observed as a rosette but has never been observed in bloom.

Since 1975 migrations of certain mesic species into the wet-mesic habitat are observable, apparently in response to the lowering of the water table. *Andropogon gerardii, Petalostemum, Physostegia, Eryngium yuccifolium* and *Veronicastrum* are observed as common seedlings at the swale edges, especially in the open areas among *Carex* that have *Senecio*.

The Dry-mesic Association. The dry-mesic association is restricted to the 0.5 ha of the western tip of the prairie—15% of the total study area. Most of the dry-mesic habitat is found in mapped Peotone soil and with a microrelief approximately 0.5 m (1.8 feet) above the study base line (0) while the wet-mesic zone lies about 0.45-0.6 m (1.5-2 feet) below the same base line.

The dominant grass is *Sporobolus heterolepis*, occurring with smaller populations of *Stipa spartea, Panicum leibergii, P. agrostoides, Aristida oligantha, Koeleria cristata, Agrostis alba*, and *Bromus kalmii*. These are rare or absent elsewhere in the prairie. Some of the above species have western affinities. A subdominant grass in the dry-mesic area is *Andropogon scoparius.*

From aerial photos (1982) of the site, the dry-mesic soil sites seems to be the least disturbed. The dry-mesic section appears as a small plateau extending into a mesic/wet-mesic area. The sloping edge of this plateau is rather abrupt, representing approximately a 0.3-m (1-foot) change in the microrelief.

Notable forbs include *Asclepias tuberosa* (occasional), *Lilium philadelphicum andinum* (rare), *Aster azureus* (common), *Amorpha canescens* (infrequent), *Coreopsis palmata* (colonial), and *Helianthus mollis* (colonial). These species co-exist within the *Sporobolus* community.

Most of the mesic species are also found here, thus species diversity is relatively high.

Natural areas quality. Applying the numerical Rating Index for natural areas (Swink and Wilhelm 1979) to the CRP, and using the latest prairie species inventory for Oak Lawn (1975), a Rating Index (I) value of 58.7 is derived (109 taxa, with a mean rated quality of 5.62). Using the 1981 survey of taxa at CRP produces a Rating Index (I) of 72.84 (153 taxa, with a mean rated quality of 5.89), placing this prairie among the top natural areas in the Chicago region. Unfortunately, no management or preservation plans are known to exist for this privately owned site. There is, consequently, no guarantee that this remnant will not be destroyed in the same manner as the rest of the site.

ACKNOWLEDGMENTS

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APPENDIX 1. THE EXISTING PRAIRIE FLORA REPORTED FOR THE CHICAGO RIDGE PRAIRIE (1981), WORTH TOWNSHIP, COOK COUNTY, ILLINOIS.

EQUISETACEAE
- *Equisetum arvense*
- *E. hyemale affine*
- *E. hyemale intermedium*

GRAMINEAE
- *Agrostis alba*
- *Andropogon gerardii*
- *A. scoparius*
- *Aristida oligantha*
- *Bromus kalmii*
- *Calamagrostis canadensis*
- *Elymus canadensis*
- *Koeleria cristata*
- *Panicum leibergii*
- *P. virgatum*
- *Phalaris arundinacea*
- *Poa pratensis*
- *Sorghastrum nutans*
- *Sporobolus heterolepis*
- *Spartina pectinata*
- *Stipa spartea*

CYPERACEAE
- *Carex* spp. (2)
- *C. buxbaumii*
- *C. stricta*
- *C. tetanica*
- *C. umbellata*
- *Eleocharis compressa*
- *Scirpus lineatus*

COMMELINACEAE
- *Tradescantia ohiensis*

LILIACEAE
- *Allium canadense*
- *A. cernuum*
- *Lilium michiganense*
- *L. philadelphicum andinum*
- *Smilacina stellata*

AMARYLLIDACEAE
- *Hypoxis hirsuta*

IRIDACEAE
- *Iris virginica shrevei*
- *Sisyrinchium albidum*

ORCHIDACEAE
- *Cypripedium candidum*
- *Spiranthes cernua*

SANTALACEAE
- *Commandra richardsiana*

POLYGONACEAE
- *Polygonum* sp. (1)

RANUNCULACEAE
- *Anemone cylindrica*

SAXIFRAGACEAE
- *Heuchera richardsonii grayana*
- *Saxifraga pensylvanica*

ROSACEAE
- *Fragaria virginiana*
- *Rosa arkansana suffulta*
- *R. carolina*

LEGUMINOSAE
- *Amorpha canescens*
- *Desmodium canadense*
- *D. illinoense*
- *Lathyrus palustris linearifolius*
- *Lespedeza capitata*
- *Petalostemum purpureum*

OXALIDACEAE
- *Oxalis violacea*

POLYGALACEAE
- *Polygala verticillata isocycla*

EUPHORBIACEAE
- *Euphorbia corollata*

HYPERICACEAE
- *Hypericum* sp. (1)

Appendix 1, continued.

VIOLACEAE
- *Viola papilionacea*
- *V. pedatifida*

LYTHRACEAE
- *Lythrum alatum*

ONAGRACEAE
- *Oenothera pilosella*

UMBELLIFERAE
- *Cicuta maculata*
- *Eryngium yuccifolium*
- *Oxypolis rigidior*
- *Zizia aurea*

PRIMULACEAE
- *Dodecatheon meadia*
- *Lysimachia ciliata*
- *L. quadriflora*

GENTIANACEAE
- *Gentiana andrewsii*
- *G. quinquefolia occidentalis*

APOCYNACEAE
- *Apocynum androsaemifolium*
- *A. cannabinum*
- *A. sibiricum*

ASCLEPIADACEAE
- *Asclepias hirtella*
- *A. purpurascens*
- *A. syriaca*
- *A. tuberosa*
- *A. viridiflora*
- *A. verticillata*
- *A. sullivantii*

CONVOLVULACEAE
- *Convolvulus sepium*
- *C. spithameus*

POLEMONIACEAE
- *Phlox glaberrima interior*
- *P. pilosa*

BORAGINACEAE
- *Lithospermum canescens*

VERBENACEAE
- *Verbena hastata*

LABIATAE
- *Blephilia ciliata*
- *Lycopus americanus*
- *Monarda fistulosa*
- *Physostegia virginiana*
- *Pycnanthemum tenuifolium*
- *P. virginianum*
- *Satureja arkansana*
- *Scutellaria parvula*
- *Stachys tenuifolia hispida*
- *Teucrium canadense*

SOLANACEAE
- *Physalis heterophylla*

SCROPHULARIACEAE
- *Castilleja coccinea*
- *C. coccinea* forma *lutescens*
- *Gerardia tenuifolia*
- *Penstemon pallidus*
- *Veronicastrum virginicum*

RUBIACEAE
- *Galium boreale*
- *G. obtusum*

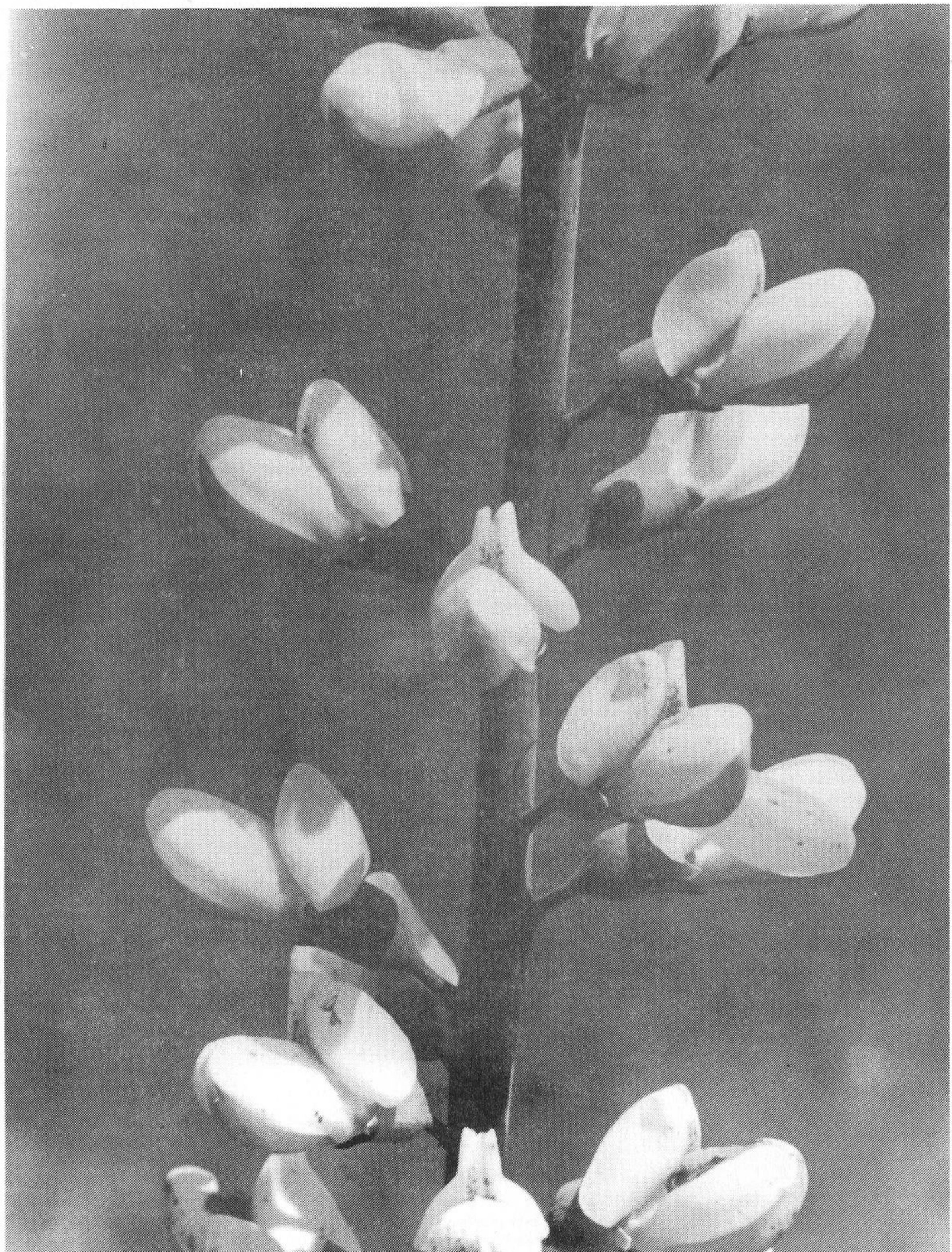
VALERIANACEAE
- *Valeriana ciliata*

CAMPANULACEAE
- *Campanula aparinoides*

LOBELIACEAE
- *Lobelia spicata*

COMPOSITAE
- *Achillea millefolium*
- *Antennaria neglecta*
- *A. plantaginifolia*
- *Aster azureus*
- *A. ericoides*
- *A. laevis*
- *A. novae-angliae*
- *A. pilosus*
- *A. ptarmicoides*
- *Bidens* sp.
- *B. coronata*
- *B. polylepis*
- *Cacalia tuberosa*
- *Cirsium discolor*
- *C. hillii*
- *Coreopsis palmata*
- *C. tripteris*
- *Erigeron philadelphicus*
- *Eupatorium altissimum*
- *E. maculatum*
- *E. perfoliatum*
- *Eupatorium serotinum*
- *Helenium autumnale*
- *Helianthus grosseserratus*
- *H. mollis*
- *H. occidentalis*
- *Krigia biflora*
- *Liatris aspera*
- *L. spicata*
- *Parthenium integrifolium*
- *Prenanthes racemosa*
- *Ratibida columnifera*
- *R. pinnata*
- *Rudbeckia hirta*
- *Senecio aureus semicordatus*
- *S. pauperculus balsamitae*
- *Silphium integrifolium*
- *S. laciniatum*
- *S. terebinthinaceum*
- *Solidago altissima*
- *S. gigantea*
- *S. graminifolia meadia*
- *S. graminifolia nuttallii*
- *S. nemoralis*
- *S. riddellii*
- *S. rigida*
- *S. juncea*
- *Vernonia fasciculata*
- *V. missurica*

Part 4. Reconstruction, Preservation, and Management



A BACKYARD PRAIRIE

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Abstract. Details of the planning and execution of a modest prairie restoration are related. A spacing device, the planting board, is described. Project planning methods are reviewed and prairie species selected for the restoration are briefly noted.

INTRODUCTION

In February 1968, I attended a medical conference in Denver, Colorado. While there, I decided to visit the U.S. Mint, but when I arrived it was closed to visitors. I was thus left with an hour to wait for the next bus home. I decided to spend the time taking a short walk. While on my stroll, I came upon a bookstore that prominently displayed in its front window a work entitled *A Sand County Almanac* by Aldo Leopold. I bought the book and read it the next day and many times since.

Leopold referred to a prairie plant by the name of *Silphium laciniatum* (compass plant) as one of the vanishing prairie species. Not having the slightest idea what he was referring to, I set out to discover for myself what the plant was. I now have several fine specimens of *Silphium laciniatum* growing in my back yard. In seeking to learn more about this flower, it was only natural that my interest in the prairie would follow. By 1975, I was ready to plant my first backyard prairie. I began to collect seed for my project that autumn.

MY BACKYARD PRAIRIE

In early May 1976, I roto-tilled two strips of lawn and cleaned out the grass roots by hand to prepare the seed beds. The 2 strips were 3 × 32 feet and separated by 4 feet of bluegrass lawn. I broadcast my seed mixture onto the ground and raked in it. I then dug in a border of 4 × 8 × 16 inch concrete blocks around the 2 plots as a barrier to my lawn.

I played a lot with my 2 little plots over the next few years, adding more plants. One of the things I didn't like was that the tall grasses dominated the forbs.

In the summer of 1980, I felt I was ready to undertake the project of enlarging my backyard prairie. My plan was to enlarge my prairie to 16 × 32 feet, thereby encompassing the first prairie planted in 1976. This may not seem very large, but keep in mind that my entire backyard is only 30 × 50 feet. I also planned to establish a backyard prairie of forbs. These flowers would be planted among a stand of medium height grasses, with representative clumps of tall prairie grasses for completeness.

Therefore, the following projects were completed in the summer and fall of 1980 and the spring and summer of 1981:

1. The bluegrass and all but 46 square feet of my first prairie were killed by spraying with the herbicide Round-up. The spray was applied in August 1980.
2. In September 1980, the 16 × 32 feet area was roto-tilled and left fallow until the next spring.
3. From July until November 1980, seeds were collected locally for 20 species of flowers and 2 species of native grasses.
4. During the winter months, all of the seeds were cleaned, and in mid-March 1981 all of the flower seeds were stratified. I did not stratify the grass seeds.
5. In early May of 1981, I again had the site roto-tilled and raked free of debris.
6. I planted the seeds on 16 May 1981, using the planting board.

THE PLANTING BOARD

The planting board I used was constructed by the Bickelhaupt Arboretum of Clinton, Iowa, from plans and descriptions provided to them by Ray Schulenberg of the Morton Arboretum of Lisle, Illinois. It is constructed from a 2 × 8-foot piece of ¾-inch plywood. Six inches in from both ends and from each side of the board, and at 12-inch intervals from each other, in 2 rows of 8 each, 4 × ¾-inch bolts were put in place. When this board is pressed firmly onto soft ground, it makes 2 8-foot rows of holes 12 inches apart. On the edges of the board 1-inch angle irons are fastened. These structures serve to make the perimeter of the board's imprint on the soil.

In use the board is moved its own width and set down in the marks left by the angle iron at the previous location. It leaves another set of holes 12 inches from the previous set. You kneel on the board to plant the first set of holes. When these holes have been planted, the board is then moved again by handles mounted on each end. This process is repeated until the planting is complete. In this manner you will get straight rows with plantings at 12-inch intervals. This planting pattern aids immensely when it comes time to weed the prairie plot.

PLANTING METHOD

I first made a scaled plan of the site I was going to plant. I knew my prairie size was 16 × 32 feet, so I drew on paper a 16 × 32 unit grid which contained 512 coordinates. However, since I left 46 square feet of previous prairie in the center of my plot, I had only 466 holes in which to put seed. One-half of these holes were to be planted to grasses, leaving me with 233 holes for forb seeds. I decided where each flower would be planted by assigning a number to each type of forb. I then wrote that number on one of the 233 intersecting lines of my plan. I did not mix any of the flower seeds together, but planted only 1 kind at each site.

TABLE 1. Seeds used for 1981 planting and the number of sites.

SPECIES	NUMBER OF SITES PLANTED
Forbs	
Anemone virginiana, thimbleweed	10
Amorpha canescens, lead-plant	24
Asclepias tuberosa, butterfly-weed	6
Aster laevis, smooth aster	20
Dodecatheon meadia, shooting star	36
Echinacea pallida, pale purple coneflower	32
Eryngium yuccifolium, rattlesnake master	14
Euphorbia corollata, flowering spurge	8
Liatris aspera, rough blazing star	16
Liatris aspera f. *alba*, rough blazing star, white	2
Liatris pycnostachya, gayfeather	14
Liatris spicata, spike blazing star	6
Parthenium integrifolium, wild quinine	8
Petalostemum candidum, white prairie-clover	6
Petalostemum purpureum, purple prairie-clover	3
Rudbeckia hirta, black-eyed susan	6
Silphium integrifolium, rosinweed	3
Silphium laciniatum, compass plant	6
Silphium terebinthinaceum, prairie dock	3
Solidago rigida, stiff goldenrod	10
Grasses	
Andropogon scoparius, little bluestem	229
Stipa spartea, needle grass	4

I used a variety of criteria for deciding where in the plot each would go and how many of each kind of flower I wanted. For instance, I had enough *Silphium laciniatum* and *S. terebinthinaceum* seeds to put in a dozen plantings of each. However, that would be too many large plants for such a small space. I tried to space my plantings so that they were scattered or clumped throughout the prairie for what I thought might be the best effect. I planned on my map to plant 3 sites to *S. terebinthinaceum* and 6 sites for *S. laciniatum*. On the other hand, I planted 24 sites to *Amorpha canescens* because there is a high mortality rate on the very small first-year seedlings.

My wife, Judy, and my daughter, Andrea, helped me plant. Using my plans, my wife would call out the number as I came to each site. My daughter then would hand me the properly numbered bag of seed. I'd plant that seed in the proper hole, hand the bag back to my daughter and so on. The project took 3 hours.

The way to avoid the row effect when using the planting board is simple. You alternate the rows planted to grasses and forbs with each move of the planting board.

PRAIRIE PLANTS OF MY BACKYARD PRAIRIE

My prairie project of 1981 included 2 species of grasses and 20 species of forbs (Table 1). I chose to plant *Andropogon scoparius* (little bluestem) as one of my grasses. Little bluestem is a warm season native prairie grass of medium height and is very pretty, especially in the fall. It is important to me that my forbs can be readily seen in a stand of *A. scoparius.* I have a representative patch of side-oats grama (*Bouteloua curtipendula*), so I did not include this grass in the 1981 project. Experience has taught me that side-oats grama would compete too vigorously with little bluestem. A few established clumps of big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*) and switchgrass (*Panicum virgatum*) were left so that some of the tall native grasses would be represented.

I planted 13 rooted stolons of wild strawberry (*Fragaria virginiana*) in early June 1981. They were watered daily and took hold very well. These plants spread over the entire patch before the year was over. Their stems and leaves cover the bare spots between the rows and help to keep down weed growth.

Of the 20 varieties of flowers which were planted, I have identified 18 of them as being established at the end of the first year.

CONCLUSIONS

The procedure described in this paper is specifically designed to increase the chances of for the establishment of less competitive species in a prairie project. In this particular project, the primary goal was to establish a beautiful forb display. This goal was accomplished by planting the seed of each species of forb separately in one-half of the predetermined sites within the project. The other one-half of the sites were planted to *Andropogon scoparius* with a few representative sites left or planted to the tall prairie grasses and *Stipa spartea* (needle grass).

With few exceptions, the results of my backyard prairie project were almost exactly what I wanted.

A PRAIRIE SALVAGE IN AUGUST

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Abstract. In 1980, the University of Iowa bulldozed a 1-ha prairie remnant from a steep slope on campus. Because it was the only mesic remnant in the area, the author salvaged representatives of local ecotypes, on short notice in mid-August. Four methods of transplanting were used with the following results: (1) The tops of most balled and burlapped specimens died back completely, resprouted in early autumn and provided tender fare for rabbits. However, most resprouted the following spring and approximately ½ survived the next growing season (1981) as diminutive versions of the original mature specimens. Species most tolerant of this abuse included lead-plant (*Amorpha canescens*), yellow false indigo (*Baptisia leucophaea*) and rose (*Rosa* spp.). Least tolerant were mountain-mint (*Pycnanthemum virginianum*), butterfly-weed (*Asclepias tuberosa*) and white wild indigo (*Baptisia leucantha*). (2) Sod slabs cut and run over by a scraper were severely compressed, to the detriment of most of the forbs. However, many of the larger grass clumps resprouted the following spring and are very slowly recovering. (3) Turf rolls cut by a bulldozer bucket were much more viable than those produced by method 2. Over ⅓ of the small forbs and most of the grass clumps resprouted and survived the first full growing season, although partially overrun by Kentucky bluegrass (*Poa pratensis*). The most tolerant forbs were rose and lead-plant. (4) About ¼ of white wild indigo root cuttings sprouted and survived, mostly those possessing an apical bud. Considering this was the worst possible timing for a salvage, it indicates considerable resilience for some species and bodes will for dormant-season salvages.

INTRODUCTION

In 1979, a few faculty members at the University of Iowa (Iowa City, Iowa) recognized that a small, undeveloped parcel on the west edge of the campus contained a tiny mesic prairie remnant. However, as plans were being made to use it as an outdoor classroom and laboratory, it was learned that the site was already scheduled for bulldozing, to provide another access road to the new sports arena, scheduled for construction the following year. Negotiations to reroute the road failed, although the concession was offered that plants could be salvaged by interested individuals before construction began in 1981. Despite this, we were informed in August 1980 that grading of the roadway would begin immediately. Since virtually all mesic prairie landscapes in southeastern Iowa have gone under the plow, I decided to attempt a salvage of local ecotypes in the few days remaining.

Prior to bulldozing, the remnant consisted of about 1 ha of a steep floodplain wall. The Holocene soils were developed predominantly from a clay-till paleosol which outcropped along the bluff, although small increments of silty loess were also incorporated in the soils. The hillside was very steep (22-48%), which was the prime reason it had not been disturbed prior to 1980. The site faced southwest and this exposure combined with the steep slope and clayey soil produced a mesic to dry-mesic prairie.

There was insufficient time to quantify the floristic composition of the remnant. The aspect was one of a grass-dominated prairie with large patches of lead-plant and a scattering of other forbs. The remnant had probably not burned for a century and bore a thick mat of partially decomposed vegetation. This mat contained large quantities of snail shells (mostly empty) estimated at several hundred per m². The most abundant gastropod species was *Mesodon clausus.* The site was also being invaded by staghorn sumac (*Rhus typhina*), bur-oak (*Quercus macrocarpa*) and scrub elm (*Ulmus* spp.).

TRANSPLANTING

Four methods of transplanting were utilized:

1. Ball and Burlap. The "ball and burlap" method, similar to that used for young tree nursery stock, was used for 45 large forb specimens. The soil masses ranged from 25-35 cm in diameter and 35-50 cm in depth with shape depending on my perception of which would encompass the greatest root mass. These were the largest masses of soil which would hold together as a unit when burlapped, and could be carried up the slope by 1 person. These were dug the morning of August 15 and replanted the same afternoon. Even though dry, the "A" soil horizon was mellow and friable and even the "B" horizon with its extra clay was relatively easy to dig, especially with a narrow tile spade.

The forbs were transplanted into a dense synthetic prairie about 10 miles away. The new site is nearly level but elevated and well-drained. It is composed of predominantly silt-sized, loess-derived colluvium, extensively reworked in 1972 by bulldozer, and is essentially a mesic site. In 1977 it was densely planted with prairie grasses of Nebraskan origin—big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), little bluestem (*Andropogon scoparius*), switchgrass (*Panicum virgatum*) and side-oats grama (*Bouteloua curtipendula*)—plus minor forbs. The switchgrass (variety Blackwell) is gradually gaining dominance and, stimulated by 2 burns (1978, 1980), was an unnaturally dense stand in August 1980. The soils of this site were sufficiently dry and hard that the holes for emplacing the ball and burlap specimens had to be dug with a pickax, because shovels would not penetrate the soil.

The specimens were pruned severely, ranging from 65-100% removal of leaf area, to help reduce transpiration. After planting, a single watering of about 8 l per plant was provided. High temperature for the day was 93°F. That evening, a predicted rainshower provided an additional 2 cm of rain. The forbs were spaced 3-8 m apart and marked with numbered flags for later location and identification.

2. Sod Slabs. Sod slabs were cut by a pan-scraper ("Turnapul") on August 18 and planted on August 19. The slabs initially averaged 12-14 cm thickness by 140 cm width and were spread from the machine upside down. The hostility of the contractor toward anything that smacked of environmental activism was evidenced by the fact that the scaper operator managed to lay out the slabs in a pattern so that they were repeatedly run over by the tires on subsequent passes. Most of the slabs were so compressed into the landscape that they could not be pried out with a spade the next day. Nevertheless, he did miss a few and these were chopped with a square spade into 120 squares, 30 × 30 cm, compressed to 8-10 cm thickness.

The sod slabs were transplanted to a site sloping 5-8% toward the southeast. It is at the edge of a tiny, severely degraded prairie remnant once used as haulage road for construction of a dam. Much of the surface in 1980 was a bare clay-till paleosol, eroding from runoff further upslope. Scattered clumps of big bluestem and prairie dropseed (*Sporobolus heterolepis*) plus a few specimens of roundhead bush-clover (*Lespedeza capitata*) were already present. An eroded area within this site was smoothed and carpeted with the sod squares in a rectangular grid and the cracks between the sod squares filled with loose dirt.

After emplacement on the bare clay, the sod carpet was mowed to a height of 8 cm to reduce transpiration losses and the trimmings were scattered as mulch. High temperature for the day was 91°F. A grid of short stainless steel wires was inserted at the corners of the squares, for subsequent relocation of individual squares. A predicted rainfall did not materialize and the next day the site was watered once with the equivalent of 4-5 cm of rainfall in 1 hour, with considerable runoff loss.

3. *Turf Roll.* A turf roll was cut with a bulldozer bucket. A combination of complaining and threatening on 20 August, encouraged the contractor to donate a few minutes of bulldozer time to a more careful excavation of some sod. A wide, shallow, toothed bulldozer bucket was used to cut sod slabs approximately 10 cm thick. By curling over the leading edge of the initial cut as it fed into the bucket, turf rolls were formed, about 1 m in diameter × 1.3 m wide. These were unrolled again by nudging them downslope with my pickup truck and chopping the sod into approximately 30 × 30 cm squares, with a square spade.

These 120 squares were planted at the same site with the same procedures as used for the scraper sods (method 2 described above). However, the slope was 10-12% toward the southwest. High temperature for the day was 88°F. The 4-5 cm watering was followed that night by a 2-cm rain.

4. *Root Cuttings.* Root cuttings of white wild indigo (*Baptisia leucantha*) were planted. As the bulldozers stripped back the floodplain wall to lower the road grade, long roots of white wild indigo trailed over the surface like scraps of rope. Six of these roots were gathered and the upper portions, averaging 1-2 cm in diameter, were chopped into segments about 24 cm long. These were planted in my perennial garden with the tops about 2 cm below ground surface, marked with wires, mulched with wood chips, and watered thoroughly.

SURVIVAL

1. *Ball and Burlap.* The tops of the ball and burlap specimens died back immediately in almost all cases, regardless of how much leaf area had been pruned off. However, within a month or 2 most had either resprouted near the base of the stalk or sent up a separate shoot. This regrowth was considerably more succulent than the surrounding vegetation, now hardening off in the early frosts. Rabbits found this tender fare and almost all the autumn sprouts were either damaged or destroyed. The fact that each sprout stood alone in an opening in the dense grasses probably also aided its destruction because the few which escaped serious damage were those partially enclosed by tufts of prairie grass which had been trampled over the transplant. However, the following spring many of the transplants resprouted again and at this time of year were less conspicuous and suffered only minor rabbit damage. The survival of this group at the end of 1 year (August 1981) is listed by species on Table 1. Survival is defined as having at least 1 viable stem with leaves. In general, it appears that lead-plant, yellow false indigo, and rose are most tolerant of this abuse while mountain-mint, butterfly-weed and white wild indigo are least tolerant.

The last 2 species were particularly disadvantaged by possessing long, thick, fleshy roots, most of which were severed in the transplanting process. By contrast, the 3 most tolerant species have clusters of fibrous roots at shallow depths, which could be enclosed within the transplanted ball of soil. However, black-eyed susan (*Rudbeckia hirta*) is also a weedy, aggressive, fibrous-rooted plant but did not tolerate transplanting well. Most of the specimens transplanted were mature, although some were of intermediate or small size. No accurate records of original size were kept because heavy pruning was done before transplanting. However, judging from the size of the remaining stalk, original size had little effect upon survival. Perhaps the smaller plants had a more intact root system remaining, while the larger plants possessed thicker roots which provided more nutrients for resprouting. At the end of the first year, most of the surviving plants were small, the above-ground size about that expected from second year growth from seed. However, the yellow false indigo survivors resprouted dense clusters of stems 20-30 cm high, complete with flowers which later produced seed. The sample sizes for Table 1 are, of course, very small and can only be expected to indicate the most general trends and not a precise rank order of survival applicable to other projects.

2. *Sod Slabs.* The sod slabs run through the scraper were mapped after transplanting and a definite bias was built into the sample. All large forbs were absent since their

TABLE 1. Survival of "balled and burlapped" forbs (method 1), after 1 year.

Species	Number Transplanted	Number Surviving	Percent Survivors
Amorpha canescens	9	7	67
Baptisia leucophaea	5	3	60
Rosa sp.	11	6	54
Solidago rigida	4	2	50
Rudbeckia hirta	3	1	33
Lespedeza capitata	3	1	33
Pycnanthemum virginianum	2	0	0
Asclepias tuberosa	3	0	0
Baptisia leucantha	5	0	0
Totals	45	20	44

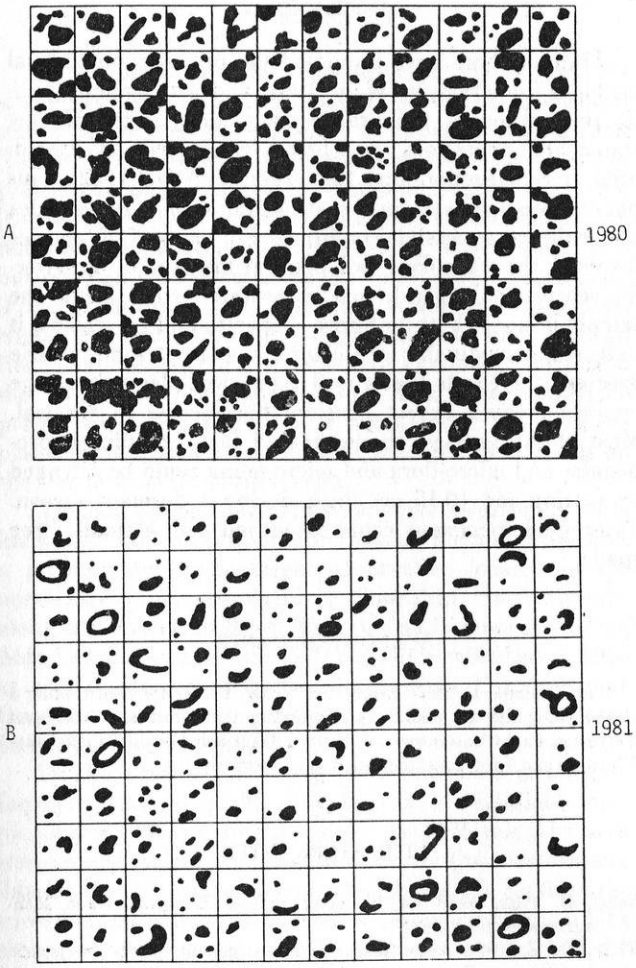

FIG. 1. Maps of grass clumps, in sod squares, transplanted by method 2.

roots were cut 12-14 cm below the surface and they simply fell out of the sod slabs. By contrast, many of the sod squares consisted mainly of 1 large clump of grass with room for little else in the square. Because of the tendency to cut out sod squares with a grass clump for a handle, the replanted area also had an unnaturally high density of plants. The forbs were studied as individual plants but grasses were in clumps with various degrees of interconnection and difficult to designate as specific individuals. Therefore, a gridded may was sketched after transplanting, which outlined the area covered by grass clumps. Seedlings and individual spears of grass were ignored. In March 1981 the plot was lightly covered with dry straw and burned so that the regrowth could be mapped again in August 1981 without interference from dead clumps that did not resprout in 1981. The grassed area maps for August 1980 and August 1981 are illustrated as Fig. 1 (A & B). These show that many of the larger grass clumps survived but are much smaller than the originals transplanted. The area covered by grass clumps 1 year later is only 36% of the original transplanted and will probably take many more years to recover. Not illustrated on Fig. 1 (B) is the growth of Kentucky bluegrass seedlings, over the entire plot. These were particularly dense in the dirt fill between sod squares. A few big bluestem and Indian grass clumps set seed after the August 1981 mowing and were easily identified. But the majority of grasses were short and not identified to species. Of the 67 small forbs originally mapped after transplanting, only 3 roses and 1 lead-plant were alive a year later. In addition, 2 roses, 1 lead-plant, 3 black-eyed susans and 1 *Baptisia* sp., appeared in locations not mapped in August 1980. These were newly sprouted seedlings and/or small plants which escaped detection in the original mapping.

3. *Turf Roll.* The sod squares cut from the turf roll were studied by the same methods as used for 2 above, with the same constraints. The change in grass-covered area is shown in Fig. 2 (A & B). Most of the grass clumps survived and areal coverage was only reduced to 68% of the original at the end of the first year. Kentucky bluegrass seedlings were abundant, as with method 2 (above). Many of the big bluestem clumps set seedheads after the August 1981 mowing but the majority of grasses remain unidentified to species. Many of the surviving grass clumps were either open in the center or crescent-shaped 1 year later. It is not clear whether this represents transplant death of the older, deeper-rooted fraction of the clump or mower damage to the higher center of the crown. A total of 54 small forbs were originally mapped in the transplanted area and their survival is listed by species in Table 2. Prairie rose and lead-plant were the most tolerant forbs. "New" specimens which grew from seed or unmapped rootstocks included 3 roses, 2

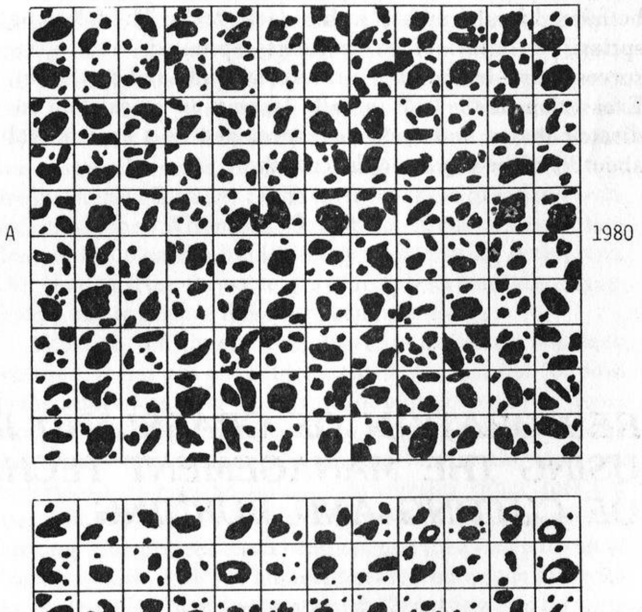

FIG. 2. Maps of grass clumps, in turf squares, transplanted by method 3.

TABLE 2. Survival of small forbs in turf roll squares (method 3), after 1 year.

SPECIES	NUMBER PRESENT	NUMBER SURVIVING	PERCENT SURVIVORS
Rosa spp.	16	10	63
Amorpha canescens	7	3	43
Rudbeckia hirta	3	1	33
Thalictrum dasycarpum	3	1	33
Baptisia sp.	6	2	33
Petalostemum purpureum	7	2	28
Pycnanthemum virginianum	2	0	0
Solidago rigida	2	0	0
Asclepias tuberosa	1	0	0
Unknown, (not common weeds)	8	0	0
TOTALS	54	19	35

lead-plants, 1 purple prairie-clover, and 1 black-eyed susan (these are not included in Table 2). By July 1982, the second year's growth contained innumerable seedlings and sprouts of native warm-season grasses plus brome grass and Kentucky bluegrass.

4. *Root Cuttings.* A total of 21 root cuttings of white wild indigo were planted. Six possessed an apical bud and the others were cut from further down the roots. Two of those with apical buds sprouted in autumn 1980 but were both cut down by rabbits within a few weeks. The following spring, a total of 6 cuttings sprouted and grew successfully—including 5 with apical buds and 1 without. Excavation of the one initially lacking an apical bud indicated that a bud node had developed at a root lateral about ⅓ of the way down the cutting.

DISCUSSION

Many authors have promoted the propagation of local ecotypes (for example, Wade 1981) and with gradual public recognition of the prairie ecosystems, some salvage/transplant operations are being conducted or considered at construction sites (for example, Nebel 1982). This paper investigates a small-scale salvage for a few species under the worst possible conditions. For many of the species involved, the transplant took place at the peak of the growing season under nearly maximum water stress. While the sample is small, both in terms of species and specimens, it indicates considerable resilience for at least some prairie species. It suggests that a well-timed, well-planned salvage operation could expect considerable success in survival. Most of the grasses, shallow-rooted forbs, seedlings, propagules and micro-flora and micro-fauna could be salvaged by cutting sod 10-15 cm thick during a dormant season. Tap-rooted specimens could be moved with a small "tree spade."

ACKNOWLEDGMENTS

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RESTORATION OF GRASSLAND IN A DEGRADED WOODS USING THE MANAGEMENT TECHNIQUES OF CUTTING AND BURNING

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Abstract. Grassland and savanna plant community types were dominant in southern Wisconsin before settlement by European immigrants. As the land was settled and fires decreased, sites which were once savanna became overgrown with trees and shrubs. An area in Sauk County, Wisconsin, on the Leopold Memorial Reserve, is an example of this phenomenon. Originally an oak barren, this site gradually became a black oak woods. The approximately 70-year-old trees on a ½-acre site were removed during 1976 followed by a spring burn in 1977. Prairie vegetation was evident that same summer; there were 42 species of forbs and 10 species of grasses covering the area. Now, 5 years later, there are more than 65 forb and 13 grass species. A comparison of the groundlayer in the black oak woods adjacent to this grassland reveals the presence of at least 5 prairie grasses including *Andropogon scoparius, Koeleria cristata,* and *Stipa spartea* along with many prairie forb species such as *Amorpha canescens, Petalostemum candidum,* and *Anemone patens.* This evidence, along with the presence of flowering grasses and forbs within weeks of the initial treatment, suggests that the immediate prairie response after cutting and burning at the site was due at least in part to the presence of prairie species from the previous oak barren/grassland community type which existed there prior to 1900. Research to test this hypothesis is now in progress.

INTRODUCTION

It has been theorized that in most climatic regions where grassland and forest coexist, fire is the mechanism which determines the presence or absence of grassland (Curtis 1959). Swift and dramatic shifts from forest to prairie caused by fire have been observed in Wisconsin (Curtis 1959). One example is that of Crex Meadows in northwestern Wisconsin (Curtis 1959, Vogl 1964). Two burns in an area covered by 20- to 30-year-old jack pine (*Pinus banksiana*)[1] and Hill's oak (*Quercus ellipsoidalis*) changed the area into a grassland within 4 years. A crown fire in another part of Crex Meadows completely destroyed the tops of the trees, and within 3 months more than 70 prairie species appeared. It is not known whether these plants came from seed on the site, from dormant plants on the site, or from invading species.

A similar phenomenon apparently has occurred on a site known as Frank's Prairie in the Leopold Memorial Reserve, a private land management cooperative located in the northeastern part of Fairfield Township, Sauk County, along the Wisconsin River (Fig. 1). The Reserve, including Aldo Leopold's Sand County farm, was established in 1968 as a model for other landowners, turning "unproductive farmland back into productive wild land" (Leopold Memorial Reserve 1982).

Frank's Prairie is located on a northwestern- to western-facing hillside (Fig. 2). The soil is a Plainfield sand (Gundlach 1980) on a 6-30% slope. In 1976 this 3-ha area was covered by oak woods dominated by *Quercus velutina* (black oak) and *Prunus serotina* (black cherry). To limit the spread of oak wilt, infested trees were removed from a 1-ha area during the winter of 1976. The site was burned the following spring. By 1977 the cleared area contained 42 forb and 10 grass species common to native prairies.

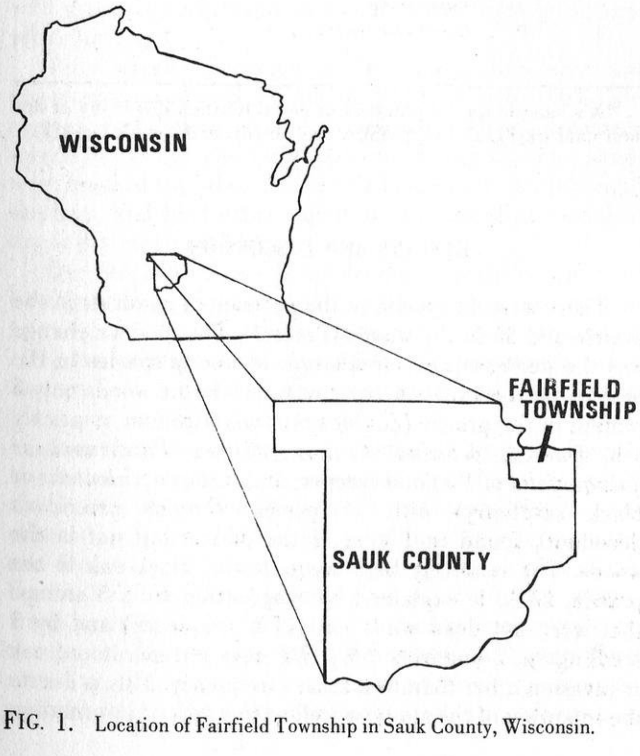

FIG. 1. Location of Fairfield Township in Sauk County, Wisconsin.

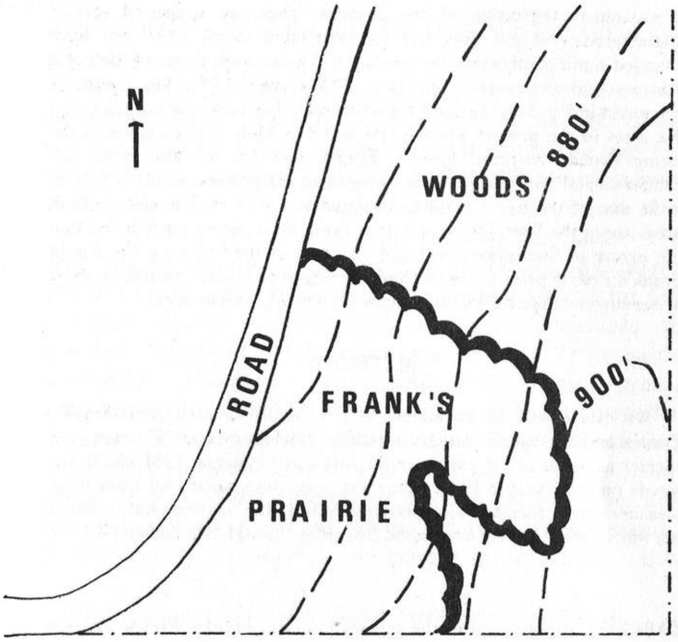

FIG. 2. Diagrammatic sketch of Frank's Prairie and the adjacent woods.

At the time of European settlement the wooded hillside containing Frank's Prairie and the Crex Meadows area were both savannas, oak and jack pine barrens respectively (Liegel 1981, Vogl 1964). Savannas and prairies were then among the most widespread plant communities in Wisconsin, probably covering 26% of the state (Curtis 1959); now they are among the rarest (Curtis 1959; Germain et al. 1977). Part of this decrease occurred as such areas became overgrown with trees, probably because of the reduction in fire frequency. Because of the rarity of these grassland communities, the Wisconsin Scientific Areas Preservation Council has placed a high priority on acquiring such areas. The change from forest to grassland described above suggests 1 way to restore these rare communities.

Although the change from forest to grassland has been reported, it has not been documented, at least not for sites in the upper midwest. The intent of our study was to document such a shift and to begin to suggest how the change occurred. If the mechanisms responsible for the shift are understood, it may be possible to identify other forested sites suitable for conversion to grassland by clearing and burning. Our project has 3 components: (1) a comparison of Frank's Prairie with the adjacent uncleared woods and with the composition of native grassland, (2) cutting and burning of an additional section of the woods and the subsequent monitoring of the results, and (3) study of the soil seed bank and of the seed rain on wooded and cleared portions of the site. This report presents preliminary results of the first part of the study.

DETERMINATION OF SIMILARITY

It was important first to determine that the woods which covered Frank's Prairie prior to 1976 was similar to the present wooded area. Because the trees in Frank's Prairie had been cut and the groundlayer vegetation had changed accordingly, we could not compare directly the

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[1] Nomenclature is from Gleason and Cronquist (1963).

pretreatment vegetation of the 2 areas. Thus, we measured several characteristics of the sites and the vegetation which would not have changed significantly since the treatment. The average slopes of each of 4 east-west transects were 9.3%, 9.7%, 12.2%, and 11.0%. The aspect, as presented in Fig. 2, is the same for both areas. The mean distance between the trees in the present wooded site is 3.8 m while that distance in the former woods covering Frank's Prairie was 4.3 m. The mean circumference of the trees (2 inches height) in the present woods is 0.91 m while that of the tree stumps in the prairie is 0.77 m. The soils in both areas are in the Plainfield sand series. From these data we concluded that the nature of the environment and structure of the woods on the site of Frank's Prairie prior to cutting and burning were similar enough to those of the current adjacent woods to allow us to make comparisons.

METHODS

We established 30 permanent 1-m² quadrats in each area, Frank's Prairie and the woods, using a stratified random system. We measured species presence in the prairie on 12 July and 17 August 1981 and in the woods on 9-10 August 1981. Frequency data were calculated from these measurements. Species which occurred outside the quadrats but in either the woods or the prairie were noted from May through September 1981.

TABLE 1. Frequencies of the species found in Frank's Prairie and the woods compared with prevalent/modal species (Curtis 1959).

% FREQUENCY					
PRAIRIE	WOODS	SPECIES	P	S	F[a]
		Grasses and Grasslike Species			
97	40	*Poa pratensis*			
63	27	*Carex sp.*			
37	7	*Stipa spartea*	X		
27	13	*Andropogon scoparius*	X	X	
17	0	*Panicum capillare*			
7	0	*Sporobolus heterolepis*	X		
7	0	*Bouteloua curtipendula*	X		
7	0	*Andropogon gerardii*	X	X	
7	3	*Koeleria cristata*	X	X	
3	3	*Sorghastrum nutans*	X		
3	0	*Elymus canadensis*			
0	7	*Danthonia spicata*			
		Herbaceous Species			
83	40	*Euphorbia corollata*	X	X	X
37	13	*Amorpha canescens*	X	X	
33	7	*Conyza canadensis*			
23	7	*Asclepias syriaca*	X	X	
23	3	*Tradescantia ohiensis*	X	X	
20	7	*Physalis virginiana*	X	X	
20	0	*Helianthemum canadense*		X	
17	13	*Aster linariifolius*		X	
17	3	*Antennaria neglecta*	X	X	
17	0	*Asclepias verticillata*	X		
17	0	*Solidago speciosa*			
13	3	*Helianthus strumosus*			X
10	7	*Tragopogon dubius*			
10	3	*Coreopsis palmata*	X	X	
10	0	*Lithospermum caroliniense*			
10	0	*Solidago gigantea*			
10	0	*Helianthus occidentalis*	X	X	
7	3	*Erigeron strigosus*	X		
7	3	*Monarda fistulosa*	X	X	X
7	0	*Solidago nemoralis*	X	X	
3	13	*Anemone patens*	X		
3	10	*Campanula rotundifolia*			
3	7	*Equisetum hyemale*			
3	3	*Monarda punctata*			
3	3	*Tephrosia virginiana*		X	
3	0	*Asclepias tuberosa*	X		
3	0	*Asparagus officinalis*			
3	0	*Petalostemum candidum*	X		
3	0	*Solidago altissima*			
0	3	*Chimaphila umbellata*			
0	3	*Hieracium aurantiacum*			
0	3	*H. scabrum*			X
0	3	*Hypericum perforatum*			
0	3	*Phryma leptostachya*			X
0	3	*Ranunculus rhomboideus*			
0	7	*Anemone cylindrica*	X	X	X
0	7	*Aralia nudicaulis*			X
0	7	*Heuchera richardsonii*		X	
0	7	*Osmorhiza claytoni*			X
0	7	*Viola pedata*	X	X	
0	7	*Smilacina racemosa*		X	X
0	10	*Circaea quadrisulcata*			X
0	20	*Taraxacum officinale*			
0	30	*Apocynum androsaemifolium*		X	X
0	36	*Comandra richardsiana*	X	X	
		Woody Species			
10	67	*Zanthoxylum americanum*			X
23	40	*Quercus velutina*		X	X
7	33	*Prunus serotina*		X	X
0	30	*Rhus radicans*			X
0	30	*Rubus idaeus*			
0	20	*Rosa carolina*		X	X
0	7	*Juniperus virginiana*			
3	7	*Parthenocissus quinquefolia*			X
0	7	*Prunus virginiana*			X
0	3	*Acer rubrum*			X
0	3	*Cornus racemosa*		X	X
20	3	*Rubus occidentalis*			X
0	3	*Smilax hispida*			X
0	3	*Vitis riparia*		X	X
3	0	*Corylus americana*		X	X

[a] X's indicate species prevalent or modal (Curtis 1959) in dry or dry-mesic prairies (P), oak barrens (S), or southern dry or dry-mesic forest (F).

RESULTS AND DISCUSSION

There were 46 species in the permanent quadrats in the prairie and 55 in the woods (Table 1). The obvious change was the decrease and elimination of woody species in the prairie. Of the 14 woody species found in the woods only 5 remain in the prairie (*Zanthoxylum americanum* or prickly ash, *Quercus velutina, Prunus serotina, Parthenocissus quinquefolia* or Virginia creeper, and *Rubus occidentalis* or black raspberry) with 1 species, *Corylus americana* (hazelnut), found in 1 area of the prairie but not in the woods. The relatively high frequency of black oak in the prairie, 23%, is explained by resprouting from 5 stumps that were not dead when cut (17% frequency) and by 3 seedlings in 2 quadrats (6%). We have not monitored oak re-invasion other than to measure frequency. This is due to the intention of the study as well as to a lack of information concerning the oak management. Although we know that the landowner has treated stump sprouts with herbicides every summer, we do not know how many sprouts were there originally, how many were treated, nor how often they were treated.

Another visible change was the increase in the grasses within the prairie. First, there is an increase in the number of grass species in the prairie (10) as compared to the woods (6). Second, 9 of the 10 grass species found within the permanent quadrats had higher frequencies in the prairie than in the woods. Moreover, 5 were not found in the permanent woods quadrats. It also has been observed that the grasses in the prairie cover much more surface area than they do in the woods.

The herbs showed definite patterns of change. The frequencies of nearly all herbaceous species listed by Curtis (1959) as prevalent (typical of a particular plant community) or modal (achieving its highest presence percentage in a particular community) in dry or dry-mesic prairies increased after cutting and burning management (Table 1). The only exceptions were *Anemone patens* (pasque flower), *A. cylindrica* (thimbleweed), *Viola pedata* (bird's-foot violet), and *Comandra richardsiana* (bastard toad-flax). Frequencies of all of the prevalent or modal species in southern dry or dry-mesic woods decreased after management with the exceptions of *Euphorbia corollata* (flowering spurge), *Helianthus strumosus* (woodland sunflower), and *Monarda fistulosa* (bergamot). Five of these exceptions occur in oak barrens as well (Table 1), reflecting their ability to survive at varying light levels.

Another way to show that the vegetation of these 2 sites now differs is to compare species found on one site but not on the other. Thirty-four species occurred in the prairie but were not encountered in the woods (Table 2). Seventeen of these (50%) are listed by Curtis (1959) as prevalent or modal in either dry, dry-mesic prairie, and/or oak barrens. Only 2 (*Rubus allegheniensis* or blackberry and *Vitis riparia* or wild grape) are prevalent or modal in southern dry or dry-mesic forests.

Fifty species occurred in the woods but were not observed in the prairie (Table 3). Thirty of these (60%) are species prevalent or modal in southern dry to dry-mesic forests or oak barrens. Only 4 (*Arenaria stricta* or rock sandwort, bastard toad-flax, *Scutellaria leonardi* or smooth small skullcap, and bird's-foot violet) are prevalent or modal in dry to dry-mesic prairies.

One other difference is the decrease in the frequency of bare ground in the area that was managed by cutting and burning. The prairie had a frequency of bare ground of 13%; the woods, a frequency of 33%. If leaf litter covering bare ground is included, the frequencies jump to 27% in the prairie and 87% in the woods.

In general the prairie is characterized by grass species in greater numbers and frequencies than the woods while the latter is dominated by greater numbers and frequencies of woody species. The prairie contains a greater number and frequency of those herbaceous species identified by Curtis (1959) as being prevalent or modal in dry to dry-mesic prairies, while the woods contains species more common to southern dry to dry-mesic forests. Although these sites have many species in common, Frank's Prairie contains 12 prairie species that are not found in the woods, and there are 26 forest species found in the woods but not in the prairie.

To assess the efficacy of cutting and burning the woods to restore native grassland, it is important to determine whether this restoration is similar in structure and species composition to a native prairie. Curtis (1959) compiled lists of 10 indicator species—species whose presence on the site can be used to describe the conditions in that stand—for each of 5 moisture levels in the remnant prairies he studied. Frank's Prairie contains 8 of the 10 indicator species for the dry-mesic prairie (thimbleweed, *Asclepias verticillata* or whorled milkweed, *Helianthus occidentalis* or western sunflower, *Panicum oligosanthes* or panic grass, *Petalostemum candidum* or white prairieclover, *Potentilla arguta* or cinquefoil, dropseed, and needlegrass); missing are *Linum sulcatum* and smooth small skullcap, the latter found in the woods. Five of the dry indicator species are found there (little bluestem, pasque flower, sideoats grama, *Petalostemum purpureum* or purple prairieclover, and

TABLE 2. Species observed in Frank's Prairie but not in the woods.

SPECIES	P	S	F[a]
Woody Species			
Rhus glabra	X	X	
Rubus allegheniensis			X
Vitis riparia			X
Grasses and Grasslike Species			
Bouteloua curtipendula	X		
Carex normalis			
C. lanuginosa			
Cyperus filiculmis			
Panicum capillare			
P. oligosanthes	X		
P. praecocius		X	
P. virgatum			
Herbaceous Species			
Achillea millefolium		X	
Artemisia campestris ssp. *caudata*	X	X	
A. ludoviciana	X		
Asclepias verticillata	X		
Asparagus officinalis			
Desmodium canadense			
Gnaphalium obtusifolium			
Helianthemum canadense		X	
Lechea intermedia			
Lespedeza capitata	X	X	
Liatris aspera	X	X	
Liatris cylindracea	X		
Melilotus alba			
M. officinalis			
Oenothera biennis	X	X	
Penstemon gracilis		X	
Petalostemum purpureum	X		
Potentilla arguta	X	X	
Senecio pauperculus			
Sisyrinchium campestre	X		
Solidago altissima			
S. speciosa			
Verbascum thapsus			

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[a] X indicates species prevalent or modal (Curtis 1959) in dry or dry-mesic prairies (P), oak barrens (S), or southern dry or dry-mesic forest (F).

Solidago nemoralis or early goldenrod), and only 2 of the mesic indicator species (*Liatris aspera* and *Ratibida pinnata*). The dry-mesic prairie seems to match Frank's Prairie in terms of indicators.

TABLE 3. Species observed in the woods but not in Frank's Prairie.

SPECIES	P	S	F[a]
Woody Species			
Acer rubrum			X
Carya ovata			X
Cornus racemosa		X	X
Juniperus communis			
J. virginiana			
Parthenocissus quinquefolia			X
Pinus strobus			
Prunus virginiana			
Quercus macrocarpa			X
Rhus radicans			X
Rubus idaeus			
Smilax hispida			X
Tilia americana			X
Grasses and Grasslike Species			
Bromus ciliatus			
Carex blanda			
C. foenea			
Herbaceous Species			
Aquilegia canadensis			
Apocynum androsaemifolium		X	X
Aralia nudicaulis			X
Arenaria stricta	X		
Chimaphila umbellata			
Circaea quadrisulcata			X
Cirsium vulgare			
Comandra richardsiana	X	X	
Desmodium glutinosum			X
Equisetum hyemale			
Erigeron pulchellus			X
Eupatorium rugosum			X
Fragaria virginiana		X	X
Galium triflorum			X
Geum canadense			X
Heuchera richardsonii		X	
Hieracium scabrum			X
Houstonia longifolia			
Krigia biflora		X	
Monotropa uniflora			
Osmorhiza claytoni			X
Pedicularis canadensis			
Phryma leptostachya			X
Polygonatum biflorum		X	X
Potentilla simplex		X	
Pteridium aquilinum		X	X
Pyrola elliptica			X
Ranunculus rhomboideus			
Scutellaria leonardi	X		
Smilacina racemosa		X	X
S. stellata		X	X
Taraxacum officinale			
Vaccinium angustifolium			
Viola pedata	X	X	

[a] X's indicate species prevalent or modal (Curtis 1959) in dry or dry-mesic prairies (P), oak barrens (S), or southern dry or dry-mesic forest (F).

The average number of species present in the 66 dry-mesic prairie stands studied by Curtis is 55. Since this number is based on data obtained from 1-m^2 quadrats, it is comparable to that obtained in the quadrat study of Frank's Prairie—46 species. Of Curtis's 55 species, 38% are present in the prairie quadrats while 64% are present somewhere on the prairie.

The "major dominant species" of the dry-mesic prairie stands studied by Curtis are grasses, in particular, little bluestem, big bluestem, needle grass, dropseed, and sideoats grama, all of which are found on Frank's Prairie. The "most prevalent groundlayer species" in his study are *Euphorbia corollata, Amorpha canescens, Solidago nemoralis, Rosa* sp., and *Petalostemum purpureum.* These first 3 are found in the quadrat study of Frank's Prairie, but all 5 have been observed on the prairie.

An interesting note is that Frank's Prairie has species which link it to oak barrens. Curtis found that there are some species that are somewhat restricted to this particular community: *Artemisia campestris* spp. *caudata, Lupinus perennis, Aster linariifolius, Helianthemum canadense, Tephrosia virginiana,* and *Viola pedata.* The presence of all but *Lupinus* gives added support to the assumption that this area in the past was an oak barrens. The index of similarity between oak barrens and dry-mesic prairie is 58, based on a scale of 0 to 100, nothing in common to everything in common, respectively (Curtis 1959: 338-339, 570-571).

CONCLUDING REMARKS

The results presented in this paper confirm that cutting the trees and burning the groundlayer can help to transform a woods into a prairie on some sites. This restoration seems to be similar in species composition to the native grasslands studied by Curtis.

It would be helpful for land managers, restorationists, and preservationists to be able to identify sites suitable for prairie or savanna restoration through this kind of management. Knowing the mechanisms responsible for the instantaneous prairie response may provide this predictive ability. Are the prairie plants dormant in the soil in the woods; are they "holdovers" in a dwarfed form; do they germinate from seeds already on the site; do they germinate from invading seeds? Answers to these questions would provide ways to evaluate sites in the forest/prairie transition zone in terms of their potential for conversion to prairie or savanna. For example, if holdovers from a former prairie are more responsive to this restoration method than is invading seed from a nearby prairie source, wooded sites which have these holdovers in the understory would have more potential for a rapid prairie restoration than wooded sites without them. Frank's Woods contains some characteristic prairie species (such as *Andropogon scoparius, Koeleria cristata, Stipa spartea, Amorpha canescens, Petalostemum candidum,* and *Anemone patens*) providing some evidence that conversion from woods to prairie is more dependent on the presence of holdovers in the understory than on other methods.

Our study is continuing in order to find the answers. Another area of the woods has been cleared and burned. Seed traps are being used to monitor seed invasion. We are documenting the changes in species composition which are taking place in this newly cleared and burned area and trying to determine the origin of the new plants which appear. The seed bank of the woods is being determined. If these answers are found, they will provide important predictive information for land preservationists, restorationists, and land managers.

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A PRAIRIE GARDEN

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Abstract. Where no natural prairie is available, the best way to learn about it is to develop one's own. I bought my lot in 1951. The native grasses arrived without my help but I introduced the forbs. Some forbs are more difficult to transplant than others. Some try to occupy the entire area and need restraining. I mow my prairie in November. I don't burn, hence trees immigrate readily. They must be removed with their roots as soon as they are discovered. To manage one's own prairie requires a sustained effort. It is instructive and a huge pleasure.

INTRODUCTION

It is instructive and a real pleasure to visit a prairie and to observe the many grasses and forbs in their different stages of development. To identify many, or at least a few, species gives one some sense of satisfaction; it is like greeting old friends. However, few people can enjoy such delights, usually because there is no good prairie close enough at hand. Observations and discussions such as those at the North American Prairie Conferences are very useful but also limited in their scope. The answer for those who have a sunny garden or yard is to create their own prairie. For most of us, this is the only way to discover how a prairie functions, and why our efforts so easily lead to failures. The natural tallgrass prairie lives on and on in all its splendor, but that is not the way it works at home. A sustained effort is needed to allow a "synthetic" prairie to evolve into something approaching a real prairie.

Northeastern Kansas, where I live, is part of the tallgrass prairie region. Its climate is sufficiently humid to permit many tree species to become established and to spread, but periodic fires keep them at bay and permit the natural tallgrass prairie to survive and flourish. Whoever wishes to develop a prairie must appreciate such basic facts.

MY PRAIRIE

I bought my lot in 1951 and set aside for my prairie an area approximately 35 by 18 m (114 × 60 feet). The land was plowed when I bought it. I was out of town most of the summer of 1952 and did nothing to start my prairie. Upon my return at the end of the summer, the land was thickly covered with bindweed (*Convolvulus arvensis*), flowering profusely every morning. I counted 14 different color patterns in the flowers, and I loved it. However, the bindweed is not a prairie plant but a European immigrant; it is considered a noxious weed that is difficult to combat.

In the spring of 1953, I observed the arrival of big bluestem (*Andropogon gerardii*) and Indian grass (*Sorghastrum nutans*). As the years went by, more and more native grass species appeared without help. Today, there is much big bluestem, Indian grass and switchgrass (*Panicum virgatum*). These tall grasses like my prairie and grow tall indeed. The greatest height ever reached by a big bluestem in my prairie was 2.80 m (over 9 feet)! Little bluestem (*Andropogon scoparius*) is less common, as are needle grass (*Stipa spartea*), side-oats grama (*Bouteloua curtipendula*) and numerous others. Two European immigrants, Kentucky bluegrass (*Poa pratensis*) and brome grass (*Bromus inermis*) also became established in spots.

In that same spring of 1953, I transplanted forbs from nearby natural prairies into my own. I soon learned, however, that I had to face some problems. For instance, lead-plant (*Amorpha canescens*) consistently died when I transplanted it. Others did well, sometimes even better than in their original home. For instance, hoary puccoon (*Lithospermum canescens*) produced anywhere from 2 to 8 flowering stems per plant in the natural prairie but 8 to 16 stems in mine. Some forbs soon began to spread on their own accord, like the New England aster (*Aster novae-angliae*), some alliums, wild blue phlox (*Phlox divaricata*) and downy phlox (*Phlox pilosa*).

Some forbs seemed to believe that I introduced them into my yard so they could take it over. They spread rapidly, crowding out all others, and I have been fighting them ever since. It seems practically impossible to get rid of them short of spraying them with a herbicide. This I have not been prepared to do. The sunflowers (*Helianthus* spp.) are the worst offenders, especially downy sunflower (*Helianthus mollis*) with its long underground rhizomes and compass plant (*Silphium laciniatum*) with its taproot.

My grasses and forbs are now doing well. The most desirable ones have a chance to develop while the most aggressive ones are being restrained. As the more desirable forbs become larger and more numerous, the competition among them becomes keener and gradually some of them begin to suffer. For instance, heath aster (*Aster ericoides*) at first spread so rapidly, it soon became a candidate for removal. But I did nothing about it and gradually it diminished. Not much of it is left. The puccoon plants are smaller now and some have disappeared altogether, much to my regret. The same applies to the alliums, butterfly-weed (*Asclepias tuberosa*) and black sampson (*Echinacea angustifolia*). The beautiful cobaea penstemon (*Penstemon cobaea*) has disappeared. It means, as I have learned belatedly, that some species must be protected from too much competition or else they will be crushed.

Other forbs are doing very well, holding their own without spreading excessively. Among these are 3 species of wild indigo (*Baptisia leucophaea, B. leucantha, B. australis*), the phloxes mentioned above, prairie coneflower (*Ratibida pinnata*), Canada anemone (*Anemone canadensis*), spiderwort (*Tradescantia bracteata*), gayfeather (*Liatris squarrosa*), and many others.

Competition in a natural prairie is keen but kept within limits by occasional fires and repeated grazing. The absence of fire and grazing from my prairie leads to uninhibited growth with the resulting increase in competition. The bindweed disappeared long ago along with other weeds like dandelions. I never combated them; the native grasses and forbs did that far more effectively than I could have without herbicides. The very wet spring and early summer of 1982 resulted in a massive growth, with a height and density never reached before, but with relatively few flowers. Only the prairie coneflower put on a spectacular show.

Late in the fall, when the growing season is over, I mow my prairie with a rotary mower that shreds everything. This is hard work and takes a lot more time than mowing the front lawn. But in the end, the area is clean and smooth. The shredded material remains on the ground, forming a mulch.

I never burn my prairie. As a result, a host of tree seedlings becomes established every year, mainly elm, oak, and mulberry. At first, I thought nothing of it, knowing they would be mowed off in the fall. However, by then they were dormant and mowing did not hurt them. The following spring saw them produce new shoots from a root system that had remained intact. Again I let them be, and again they were mowed off. By the third year, however, the root system was so well-developed that the new shoots quickly turned into sturdy, woody, well-branched young trees, all in one growing season. They had to be removed with a saw! The lesson: pull them out with their roots when they first appear.

The close contact with my prairie has given me much pleasure as well as a greater appreciation of the prairie as a plant community, of its ecological intricacies, and of its beauty. Managing it is satisfying because it is so instructive. Certainly, to have a prairie is worth the effort that should go into it.

MICHIGAN CEMETERY PRAIRIES AND THEIR FLORA

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Abstract. The remnant prairie flora of Michigan cemeteries is described and the possibilities for preservation are discussed. The significance of Michigan's first cemetery prairie management project at Harrison Cemetery, Prairie Ronde Twp., Kalamazoo Co. is reviewed.

INTRODUCTION AND METHODS

The prairie cemeteries of Michigan and the Midwest present a rich resource of history, natural beauty, and information concerning the original vegetation of the region.

Over 100 sites were examined in this study which concentrated in southwest Michigan where previously documented prairies exist (Butler 1947, 1948, 1949; Veatch 1928; Scharrer 1971). Locations elsewhere in southern Michigan which were previously examined by the author for historic materials and were later checked for native vegetation provided a relatively random comparison group. For the purpose of this study the term "prairie cemetery" includes any cemetery with any significant amount of native grassland flora. No attempt is made to recognize a subcategory of savanna or oak-opening cemetery.

These sites are found in a variety of locations including dusty roadsides, among fields of corn, in small remaining groves near early homesites and on the edges of landfill dump sites. Most often they are under shadowy planted pines on the edges of original prairies or in sites originally occupied by oak openings. The great number of prairie cemetery sites found both on the edge of "historic" prairie areas and at great distances from traditionally recognized prairies and notably in southeast Michigan, suggest that native grassland plants were widely distributed within the state at the time of settlement, or that plants of these communities spread rapidly after forests were cleared during the years of first settlement (Pleznac 1980).

Examination of Michigan cemetery sites for original flora begins with the premise of, it should be there. Locating the cemetery on a topographical map or in the reference source *Michigan Cemetery Compendium* (1979) implies that prairie could be there. But the true test is to pull out a county map, visit the site, walk the fencerows, examine the plots close to the gravemarkers and learn to recognize the vegetation in a minute, mowed form.

Visits at different times of the year can give varying impressions to the investigating botanist. In Michigan, a good cemetery prairie indicator is the early buttercup, *Ranunculus fascicularis.* Because of its early season emergence in April or May and its small stature, it often eludes mowers and thus provides a clue to the possibilities of later season native vegetation. A second visit should be made to the site in mid-August to check for plants that may survive close to gravestones, or stand along the fencerows, or remain unmowed in the summer heat.

When traveling through the Midwest one can locate cemeteries where native vegetation is preserved and appear to burst with energy-spreading foliage as in Queen Anne Prairie Cemetery, Woodstock, Illinois; German Settler Cemetery, LaPaz, Indiana; Clay Prairie, Allison, Iowa; as well as sites in Wisconsin and Ohio. In Michigan, where 2 cemeteries are currently managed for prairie, the usual situation is that the most notable native plants are in hedgerows around the cemeteries, as those plants inside are usually kept mowed. Mowing does not totally eradicate the evidence that prairie vegetation existed here but shows that prairie now survives in only unplowed pockets.

HARRISON AND GENESSEE PRAIRIE CEMETERIES

Prairie Ronde, once the largest and perhaps the richest prairie in southwest Michigan, now contains only scattered prairie remnants in roadside ditches and in damp pockets of undrained marsh. Today, what may be the largest concentration of native vegetation on Prairie Ronde is found in the back corner of a small township cemetery, Harrison Cemetery, where some of the first settlers are now buried. In 1980, this land became the first cemetery in the state to be managed as prairie.

Concern for the remaining native vegetation on Prairie Ronde was expressed as early as the 1940s by Clarence and Florence Hanes (1947). Their view was that in some rural cemeteries remnants of the prairie flora still remained. "When the prairie was broken up for the planting of crops, the only undisturbed refuge [prairie violet, *Viola pedatifida*] had was along roadsides, in fencerows, in cemeteries, and on the right of ways of railroads. In Prairie Ronde Township it has been found in the Harrison Cemetery."

Many of the Hanes' extensive field notes on Kalamazoo Co. were stored away until prairies became popular topics for study and people began to search for the remnant landscapes. When Harvey Ballard of Vicksburg, Michigan, explored the pioneer cemetery on Prairie Ronde in the late 1970s, it was mowed on a regular basis, but on close observation the fencerows showed several native species. This suggested possibilities of additional dormant vegetation in the body of the cemetery. There in the edge, in the thick black soil, several rosinweeds, *Silphium integrifolium,* raised their sunny heads, and between the oldest part of the cemetery and the farmer's cornfield several white baptisia, *Baptisia leucantha,* bloomed, offering exciting possibilities. In the northeast corner of the cemetery early buttercup and prairie violet still persisted, as seen by the Haneses. Eventually, the Michiana Prairie Society approached the Township Board with the suggestion of leaving an unmowed corner of approximately 33 × 66 feet to see if, given an opportunity, more prairie species would reappear. The Township agreed. This was a decision that required a bit of courage from them for Michigan law makes it clear that a township board may be sued to vacate a cemetery that has become a commons, or has become neglected or abandoned, or has become a public nuisance. To avoid offending anyone who visited the site, or thought the board was being lax, a sign was erected to explain what had taken place.

By the spring of 1982, it was apparent native plants had achieved dominance. Now came the expansion of the prairie area to one-tenth of an acre and controlled burning to improve the vegetation and allow for a more natural development of the prairie. This site is now in its third year and has produced 21 typical prairie species, most notably 3 forbs on the Michigan threatened list.

North of Prairie Ronde is a cemetery on a smaller historic grassland, Genessee Prairie. Remnants should have also survived in the cemetery located here, and in the fencerows single stalks were found of spiderwort, *Tradescantia ohiensis*; butterfly weed, *Asclepias tuberosa*; and yellow coneflower, *Ratibida pinnata*; along with a clump of switchgrass, *Panicum virgatum.* Examination in spring revealed early buttercups and pussy toes, *Antennaria neglecta.* As summer approached, trimming was less careful, allowing black-eyed susans, *Rudbeckia hirta,* butterfly weed, and several white baptisia to appear at the corners of the stones.

FURTHER SITES

Locating prairie cemeteries takes time, patience and curiosity. There are locations where one would expect to find prairie vegetation, places with names like Flowerfield on the south end of Prairie Ronde, a descriptive name for the area but no indication of prairie. At Little Prairie Ronde, Cass County, vegetation possibilities exist but the township has decided that anything brushy is to be removed and thus destroyed all hedgerow remnants. Other sites on historic prairie, such as Cook's Prairie, Branch Co.; Shook's Prairie, Calhoun Co.; and Grand Prairie, Kalamazoo Co.; show no remnant vegetation.

Upper Flatbush, St. Joseph Co., would appear to be 1 of the least likely places to find prairie vegetation. Tucked behind a family vegetable garden and beside a pile of junk cars, the cemetery has small unmowed patches where big bluestem, *Andropogon gerardii,* and flowering spurge, *Euphorbia corollata,* flourish. It is by chance that this vegetation survives; one neighborhood child said, "I wish they would cut the grass better so I could put my [plastic] flowers by the stones."

In larger cities and towns, native vegetation is an unlikely commodity but the "backyards" of these cemeteries can yield unique finds. Mountain Home in Kalamazoo, has a patch of ground that is too steep to mow and thus a small community including black-eyed susans and Culver's-root, *Veronicastrum virginicum,* survives. The grounds of Oak Grove Cemetery in Coldwater, Michigan, are high above the roadway with steep banks covered with seasonally changing native vegetation creating a mass of color from the time of the roses to sunflowers. Although the vegetation consists of the more common plants, the community of Coldwater should be approached with an eye toward managing the slopes and the restricting untamable bad brush. A third location is Three Rivers, St. Joseph Co., where the pioneers were buried under oaks that overlook the river. Between the river and settlers' graves is a floodplain which abounds with prairie grasses.

Preservation and restoration of cemeteries containing prairie remnants can begin with a process as uncomplicated as decreased mowing. At Sumnerville, Cass Co., mowing is on a regular schedule, but when rain delays a cutting, the gravesites are covered with nodding wild onion, *Allium cernuum,* butterfly weed and prairie grasses. This cemetery is one of the few black-soil mesic prairies available for preservation in Michigan. The extensive native flora seen indicates that a good native vegetation could be established. In other locations, areas that have been ignored for some time flourish with plants typical to the soil structure. Cavanaugh Road, near Coldwater, has New Jersey tea, *Ceanothus americanus,* bergamot, *Monarda fistulosa,* blazing star, *Liatris aspera,* and flowering spurge among others. Close to the gravesites can be seen promise of more prairie if it were only allowed to develop. The steep slopes of Mount Hope Cemetery, Barry Co., have produced spiderworts, blazing stars, prairie phlox *Phlox pilosa,* butterfly weed, and sunflowers *Helianthus* spp., all in a large dramatic hillside cemetery. Johnson Cemetery, Hillsdale Co., which may appear dull in front, has thick stands of big bluestem and samplings of the prairie species of summer in an unmowed area at the back.

Currently under informal preservation as of July 1982 is the City of St. Joseph's Brown School Road Cemetery, a dry-mesic site near the Lake Michigan shoreline. The last burials here were in 1932. Mowing has been limited, with outlying areas being generally ignored. A walk through the preserved 2-acre plot on a July afternoon led to the discovery of 36 species. By August, another 11 species had emerged.

CONCLUSION

In an old graveyard on Prairie Ronde, there was once a marker that read, "He plowed the first furrow on this prairie or in this county" (Butler 1947, 1948, 1949). Because of vandalism and lack of attention the stones at this site have been broken and pieces now reside in the basement of the local museum. As they deteriorate and break into fragments, the stones can be stored but the prairie cemeteries they marked cannot be safely packed away. They can only be preserved and maintained where they now exist if someone will notice or care.

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MANAGEMENT AND NATIVE SPECIES ENRICHMENT AS AN ALTERNATIVE TO PRAIRIE RECONSTRUCTION

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Abstract. Attempts at reconstructing prairie plant communities on bare ground have practical limitations in size, richness, and authenticity. Management and native species enrichment of existing native grass stands, old fields, and degraded prairies provide an alternative that can work with ongoing local processes. This approach can result in larger prairie simulations and, in the right conditions, more complex native grassland recreations than those developed by the typical prairie reconstruction

Certain techniques for reconstructing prairie plant communities on bare earth have gained widespread use in recent years (Rock 1974, Smith 1980, Schramm 1970). As effective as these methods are in quickly establishing reconstructed prairies, alternative approaches to establishing native grasslands including management and native species enrichment of old fields, native grass stands, and degraded prairies should not be overlooked. In the right circumstances, management and enrichment may be less expensive, more true to local conditions, and more likely to result in a rich prairie community. At the very least, the use of this low-intensity method is philosophically appealing to the ecologist because it offers another answer to the problem of establishing complex native grasslands. Diversity in methods, as in all things, ought to be fundamental to ecology.

Prairie reconstruction[1] on bare ground is essentially a labor-intensive process which aims to impose profound and rapid change on a site. Unfortunately, fast establishment tends to limit a plant community's complexity and to simplify its structure (Schwartzmeier 1973).

In preparation for planting, the typical prairie reconstruction site is tilled several times and herbicide is applied at least once. The effect of this on soil texture and microorganisms is largely unknown. Seed is planted either mechanically or by hand, either method causing general soil compaction. The seed used, whether collected or purchased, is often selected without due care because of the time constraint that comes with having to cover a planting area completely with nearly all desired species in 1 season. Common mistakes in seed selection include overplanting tall grasses and aggressive forbs, omitting difficult or less obvious species such as sedges, rushes, early season forbs, and minor grasses (Zimmerman 1972), and inclusion of ecotypes poorly suited to the site because of geographic (Schramm 1978) or site-characteristic variance or hybrid hardiness (Anderson 1956, Stebbins 1966).

A major advantage of managing an existing native grassland is that there is no immediate need to establish native cover for prairie species. This matrix should be in place, although alien elements may be prominent. In time, fire and selective weeding should encourage native species expansion (Reed and Schwarzmeier 1978). With little need to suppress weeds or to develop a native grass cover, more effort can be directed at well-considered selection of seed and propagation of "difficult" prairie species, seed gathering, and project evaluation. In following this approach the prairie worker has the luxury of having local grassland processes work for him.

Given the availability of a large degraded prairie, native grass stand, or old field with native elements, the possibility arises for creating or improving habitat for indigenous insects, birds, and mammals which may require larger ranges than those afforded by the typical prairie reconstruction. Large xeric areas with considerable native species content still persist even in unlikely regions like southwestern Michigan (Chapman and Pleznac 1981). Relative stability, richness, and the chance for recruitment of volunteer plants from local sources should increase with the size of the management area. Although xeric areas seem to be easier to enrich with native species in my experience, some work has been done in adding forbs to established tallgrass stands (Schramm 1978). Expansion of existing tallgrass remnants using seed from the remnants themselves has been proposed by some authors and should be considered by managers. In addition to creating reconstructed prairie areas of some intrinsic value, this tactic should have positive effects upon the long-term stability and richness of the original remnant as the additional area should serve as a buffer and provide other benefits to the original site.

Because native remnants deserve protection from well-meaning alteration, enrichment is not a proper technique on any site which is a high-quality remnant nor is it advisable on any site which has not been thoroughly inventoried for a full season.

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[1] What is here termed "reconstruction" is often referred to as "restoration." But what is prairie "restoration?" If you bought an antebellum home and had it bulldozed and rebuilt from a blueprint, would you be restoring it? No, this is clearly reconstruction. In the same manner, when a grassland is plowed and treated with herbicide to make way for a simulated prairie, "restoration" is scarcely descriptive of the management process. "Restoration" is particularly objectionable when used to describe work with prairie materials in geographic areas or sites which never supported native grasslands. I suggest use of the term "reconstruction" for all prairie simulations in which the plant community is put together essentially "from scratch." This is more than a semantic nicety. The term "reconstruction" is a reminder of the basic artificiality of this process. Use of this terminology can help prairie workers to remember the limitations of the process and the product.

THE EFFECTS OF MOWING AND BURNING ON A RESTORED PRAIRIE AT PEA RIDGE NATIONAL MILITARY PARK, BENTON COUNTY, ARKANSAS

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Abstract. Representative plots of prairie established in 1975, 1976, and 1978 on formerly cultivated land and currently dominated by *Andropogon gerardii, A. scoparius, Panicum virgatum,* and *Sorghastrum nutans* were mowed in April, June, and September of 1980. Other plots were burned or designated as controls. Analysis of cover measurements made in June or September of 1980 or 1981 showed that prairie grasses grew better on mowed plots than on control plots. Also, better growth generally occurred on plots with mulch left on the ground than on plots with mulch removed, and on plots mowed in April or September compared to those mowed in June. Burning was not beneficial on all plots. Prairie grasses on most plots showed increased growth following burning, but all burn plots showed less growth 2 years later as compared to the controls. Also, burning favored large increases in weed populations. Results of this study indicate that at least for the near future the best management technique for maintenance of prairie at Pea Ridge National Military Park is mowing every 2 or 3 years and leaving the mulch on the ground.

INTRODUCTION

Periodic mowing or burning has been used for maintenance of native prairies in the central U.S. for many years. The effects of burning, mowing, or clipping have been reported for Nebraska (Weaver and Rowland 1952), Iowa (Ehrenreich 1959, Hill and Platt 1975), Missouri (Kucera and Ehrenreich 1962, Kucera 1970), Oklahoma (Penfound 1964, Rice and Parenti 1978), Kansas (Hulbert 1969, Owensby and Smith 1973) and Texas (Smeins 1973). These studies and many others indicate that decreases in productivity, changes in forb populations, poorer growth of many prairie grasses, or increases in undesirable woody species generally occur if native bluestem prairies are not periodically mowed or burned.

Although management practices used on native prairies have been applied to prairies re-established on formerly cultivated land, very little quantitative information on the effects of mowing or burning of such areas has been reported, particularly on restored prairies less than 6 years old. Exceptions include Becic and Bragg (1976) in eastern Nebraska, who suggest that burning is the most successful management technique to apply during the establishment of a native bluestem grassland and that limited mowing in conjunction with burning is also relatively successful. However, in a different experiment Dale and Smith (1979) in Arkansas report an overall decline in cover of prairie grasses and increases in weedy species 2 years after spring burning and fall mowing of restoration plots that had been established 2 years previously.

Some of the problems associated with native prairies not subject to mowing or burning such as poorer growth of prairie grasses and decreases in forb populations were beginning to become evident on 4- and 5-year-old prairie restoration plots at Pea Ridge National Military Park in 1979. Since the results of previous investigations on restored prairies did not provide conclusive evidence as to the best management procedures suitable for Pea Ridge, a study on the effects of mowing and burning was initiated in 1980 to determine the best management techniques.

PROCEDURES

In 1979, percent cover was determined for representative .405 ha (1 acre) tracts of prairie established in 1975, 1976, and 1978. In March 1980, these were subdivided into 0.025 ha (1/16 acre) plots and designated as control, burn, or mow areas.

Burning was in early April 1980 and mowing in April, June, and September. Mulch was left on the ground on half of each mow plot and removed from the other half shortly after mowing. No plot was mowed more than once. Cover determination by species was made in June and September of 1980 and 1981, approximately 1 week before mowing on all plots using a modification of the ocular point method (Winkworth and Goodall 1962).

The field data for each treatment from plots established in different years were compiled separately and converted to percent living cover of prairie grasses; weedy grasses, forbs, and woody species collectively; and non-living debris (designated here as mulch) or bare ground.

Big bluestem (*Andropogon gerardii*), little bluestem (*A. scoparius*), switchgrass (*Panicum virgatum*), and Indian grass (*Sorghastrum nutans*), are designated collectively as prairie grasses in this study.

RESULTS AND DISCUSSION

Prairie Established in 1975

Percent cover of prairie grasses in the control plots showed a marked decline from fall 1979 to fall 1980 but by fall 1981 cover had increased to near that of 1979 (Fig. 1). These changes in cover are closely correlated with weather conditions. The growing season of 1980 was unusually dry but precipitation in 1981 was near normal.

In regard to individual species, cover of big bluestem increased from 1979 to 1981 but Indian grass declined during this same period. Switchgrass showed general increases overall, and little bluestem showed little change. Fluctuations in weedy species varied considerably, and species presence and growth were closely related to rainfall during the growing season. For example, ragweed (*Ambrosia artemisiifolia*) populations increased in 1980 but beggarticks (*Bidens aristosa*), a more mesophytic species, became more prominent in 1981.

Burning caused a sharp drop in cover of prairie grasses from fall of 1979 to spring 1980. This was accompanied by increases in weedy species, and a slight decrease in bare or mulched areas. It was noted also in June 1980 that the prairie grasses were larger and darker green than those in the control plots, and the weeds were much more prominent. This was probably because of warmer soil earlier in the year and availability of increased nutrients caused by burning. By fall 1981 the grasses had increased but the cover was much less than in 1979. Weedy cover was still high but areas covered with mulch or bare areas had dropped to less than 2%. Also, the principal weedy species changed from ragweed in the dry areas and tickseed in lower, moist places in 1980 to Korean lespedeza (*Lespedeza stipulacea*) by fall 1981. These trends suggest that burning had a deleterious effect when compared to the controls (Fig. 1).

The effects of mowing depended primarily on when the mowing was accomplished and whether the mulch was removed or left on the plot. Trends in changes of prairie grass cover from 1979 through 1981 on plots mowed in April and September were similar to those of the controls (except for a slight decline between fall and spring 1981 on some plots), but the overall changes were less.

The greatest changes occurred on plots mowed in June. These changes followed the same general trends as the controls but their amplitude of change greatly exceeded the controls at comparable times. As the percent cover of grasses changed, the weeds and bare areas or areas covered with mulch generally showed opposite, concomitant changes (Fig. 1).

Plots on which the mulch was removed shortly after mowing in June and September showed greater declines in percentages of prairie grasses present by fall 1980 than plots where mulch was left on the ground. The percentages for plots mowed in April were slightly higher where mulch was removed, probably the result of faster growth following the spring mowing. By fall 1981, percentages of prairie grasses had increased considerably on all plots.

It should be mentioned that in spring and early summer it was observed that the grasses on plots with mulch removed showed better growth at first than plots where mulch was left on. This was probably in response to a warmer soil and more adequate moisture. By the middle of July, plots with mulch removed developed a soil moisture deficiency, and greater growth occurred on plots where soil moisture loss had been reduced by the mulch. This additional moisture during the latter part of the summer was probably sufficient to provide greater growth for the entire growing season.

The overall results of the experimental work on mowing of the 1975 plots suggest that mowing in April or September is beneficial to growth of prairie grasses and suppression of weeds, but mowing in June has an adverse effect, particular-

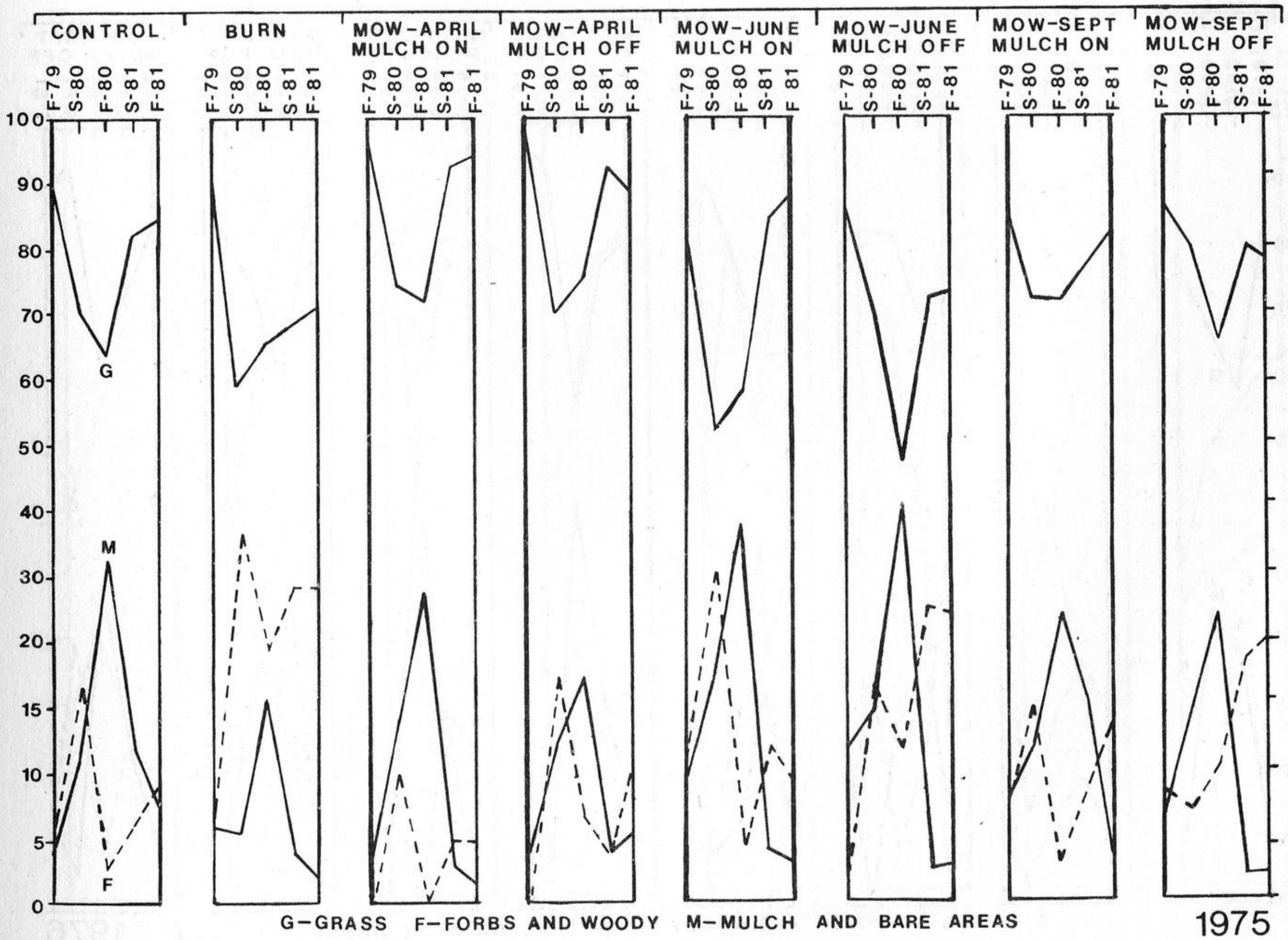

FIG. 1. Trends in growth of prairie grasses (upper solid lines); weedy grasses, forbs, and woody species collectively (dash lines); and bare areas or areas covered by mulch (lower solid lines) in control, burn, and mow plots of prairie established in 1975. Spring census is indicated by "S" and fall by "F", followed by the year. Numbers at left indicate percent cover.

ly during the year when the area is mowed. Also, removal of mulch is associated with less growth of prairie grasses and increases in weeds as compared to plots with the mulch left on (Fig. 1).

Prairie Established in 1976

Changes in cover percentages of prairie grasses in control plots between 1979 and spring 1980 were similar to those in the 1975 plots except that the lowest cover percentage occurred in fall 1980 instead of spring and there was a slight decline between spring and fall 1981. Trends and changes of weed cover and mulched or bare areas were similar until fall 1981 when small decreases in weed cover and increases in mulch cover or bare areas occurred (Fig. 2).

Results of the burning experiment show a smaller decline in cover of prairie grasses between 1979 and spring 1980 than in the controls and a greater increase until spring 1981. Also, the mulch or bare areas and weeds did not change as much. However, a sharp decline in cover of prairie grasses and a great increase in weedy species occurred by fall 1981. These abrupt changes occurred on the 1978 burn plots also, and lesser, similar changes were present on the 1976 controls and some of the mow plots at the same time. Causes of these changes are unclear, but they may be related to the slightly earlier maturation of grasses in 1981 as compared to 1980, or soil or weather conditions that increased weed growth in late summer. It appears that burning was beneficial to prairie grasses between spring 1980 and spring 1981 as indicated by the increase in cover (Fig. 2). However, the greater decline in cover between spring and fall 1981 on the burn plots as compared to the controls suggests a detrimental effect (Fig. 2).

Changes in cover of prairie grasses and weeds in mow plots during the 2 years were generally similar to the 1975 plots. Principal exceptions include constant declines in weed populations on the April plots with mulch removed, a decline from 1979 to fall 1980 and then little change in 1981 on June plots with mulch left on, and an increase in cover of prairie grasses between 1979 and spring 1981 on the April mow plots with the mulch left on. Seasonal changes in areas covered with mulch or bare areas were also similar except in the April mow plots. Results of the mowing experiment on the 1976 plots indicate overall beneficial effects of mowing in April, June, or September (Fig. 2).

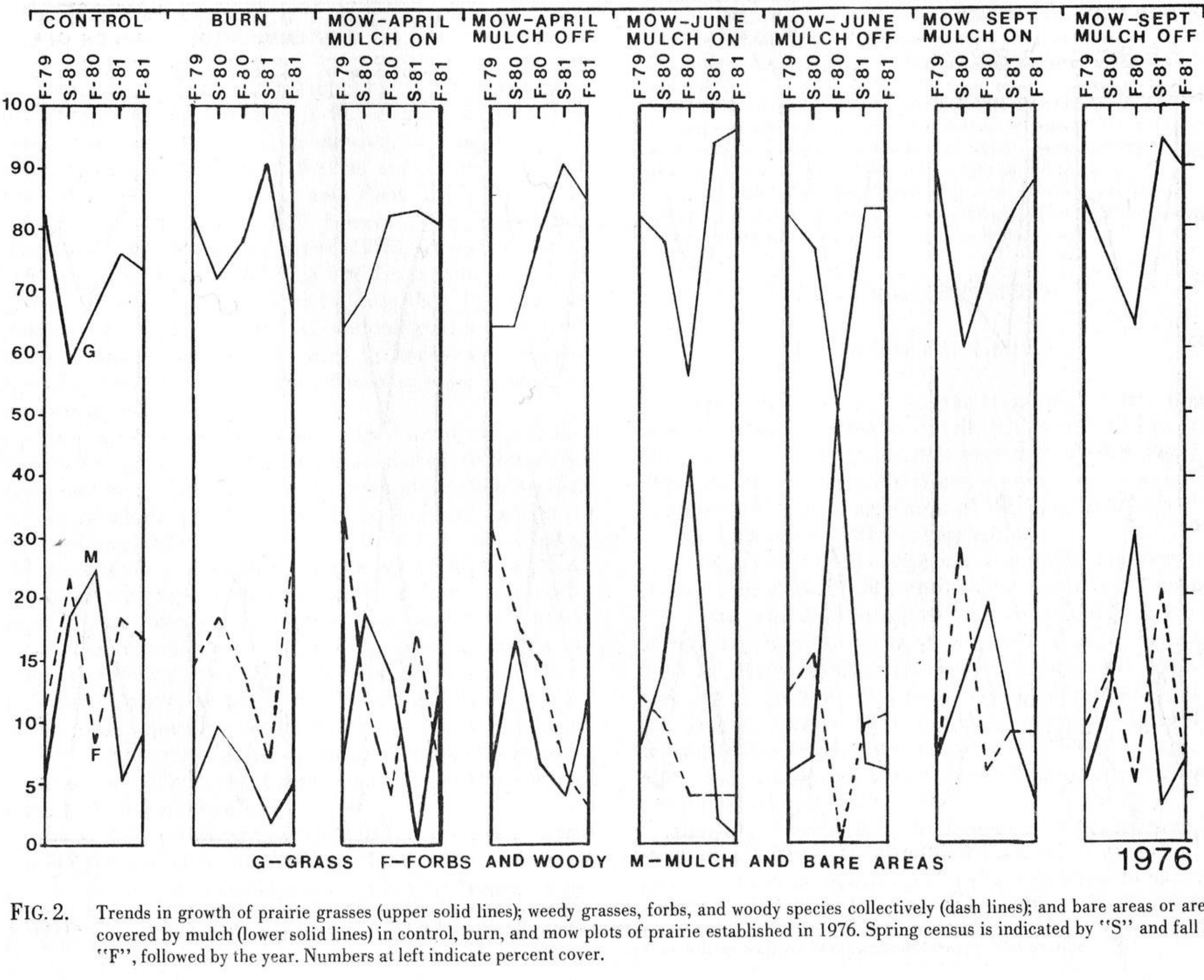

FIG. 2. Trends in growth of prairie grasses (upper solid lines); weedy grasses, forbs, and woody species collectively (dash lines); and bare areas or areas covered by mulch (lower solid lines) in control, burn, and mow plots of prairie established in 1976. Spring census is indicated by "S" and fall by "F", followed by the year. Numbers at left indicate percent cover.

Prairie Established in 1978

Percent cover of prairie grasses on control plots increased between 1979 and 1981 while weedy species and bare or mulched areas showed overall decreases (Fig. 3). Many of the changes in prairie grasses and weeds were greater in the 1978 plots than changes occurring at comparable times in the 1975 and 1976 plots. Also, in contrast to the 1975 and 1976 plots, cover of prairie grasses on all but the June mow plots constantly increased with accompanying decreases in weeds and bare or mulched areas from 1979 through 1980. The differences in the 1978 prairie compared to the older plots in 1980 can be at least partially explained by the fact that there was more space between plants and presumably less competition. During 1981, trends more closely resembled those of the older plots as the younger grasses in the 1978 plot became more mature. The effects of burning or mowing are not as well-defined as on the older plots but mowing generally appears to be beneficial. Burning is beneficial at least until the middle of the second growing season following treatment but is of questionable benefit later (Fig. 3).

All Prairie Plots

Results of this study suggest that vegetation of restored prairies at Pea Ridge National Military Park will show poorer growth if standing debris is not periodically removed. It seems questionable that burning is the best way to remove excess debris. All burn plots showed less living cover of prairie grasses present in fall 1981 than was present on control plots at the same time. Also, removal of mulch by burning apparently favored large increases in weeds either during 1980 in the 1975 plots or in fall 1981 on the other plots.

It is possible that burning could be beneficial in areas with large numbers of prairie forb seeds in the soil that germinate after burning. However, in a restored prairie that was a formerly cultivated field, such desirable effects are unlikely if mostly weed seeds are present. Unfortunately this may be the situation in many areas where restoration efforts are made.

Results of census data and observations of all mow plots suggest that the best time to mow, particularly the older plots, is in April just before "greenup." The data suggest

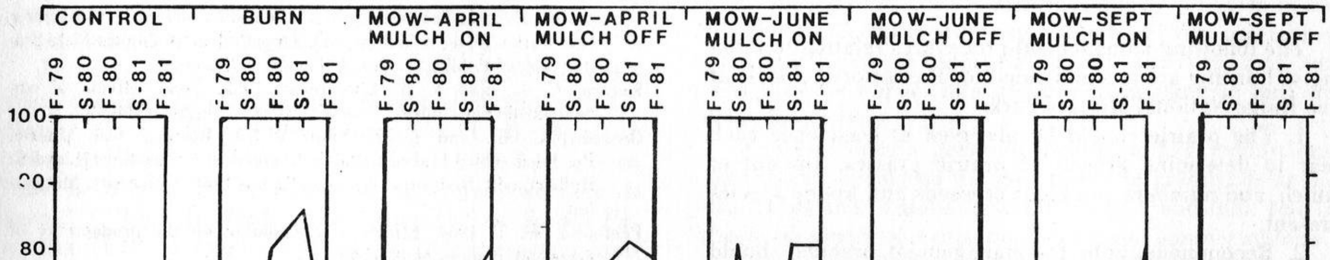

FIG. 3. Trends in growth of prairie grasses (upper solid lines), weedy grasses, forbs, and woody species collectively (dash lines); and bare areas or areas covered by mulch (lower solid lines) in control, burn, and mow plots of prairie established in 1978. Spring census is indicated by "S" and fall by "F", followed by the year. Numbers at left indicate percent cover.

also that removal of the mulch soon after the spring mowing promotes poorer seasonal growth than leaving the mulch on; however, the overall differences indicated by cover measurements were small, particularly on the older plots.

The benefits of mulch removal for prairie plant growth may depend on the weather during the growing season. Mulch removal may promote growth during cool, wet years by permitting earlier warming of the soil and evaporation of excess moisture, but mulch left on the soil may help prevent excessive moisture loss and protect the plants during hot, dry years.

The effects of mowing the older plots at the end of the growing season appeared to be only slightly less beneficial overall than mowing in April; however, removal of debris and mulch in the fall will provide decreased protection to the dormant grasses during the winter that could be detrimental. Also, weed control is less likely to be effective because foods have already been stored in roots or rhizomes, and weed seeds have been dispersed.

Mowing in June seems definitely harmful to prairie grasses during the year of mowing. The treatment may or may not control weeds depending on the weed species and growing conditions.

RECOMMENDATIONS

The following management procedures relating to mowing or burning are recommended for the restored prairie at Pea Ridge National Military Park:

1. The prairie should be observed at least once each year to determine growth of prairie grasses, amount of mulch, and numbers and kinds of weeds and woody species present.
2. Recommendations for management practice should be made yearly on the basis of the annual observations.
3. At least for the present (1982) and probably the next few years, all plots should be mowed every 2 or 3 years and the mulch left on.
4. If mulch cover later becomes excessive for good growth or prairie grasses or prairie forb populations start decreasing, then mulch should be removed shortly after mowing.
5. Burning in April should be considered if increases in woody species become a problem or mowing and mulch removal do not maintain good growth of prairie grasses and cause suppression of prairie forbs.

ACKNOWLEDGMENTS

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INVOLVING STUDENTS IN PRAIRIE PRESERVATION

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Abstract. The philosophical basis, including direct involvement and attitude change theory, for involving students in prairie preservation is discussed. Practical examples are included.

My interest in involving students in prairie preservation and restoration dates back to 1963 when I met Ray

Schulenberg of the Morton Arboretum. Ray, who had started the Arboretum prairie restoration project, helped us start our own prairie "garden" of no more than 800 square feet at Camp Reinberg near Palatine, Illinois. We worked with college students acting as part-time student teachers and 5th and 6th grade students from nearby schools.

My interest intensified when I became a member of the Faculty of Outdoor Teacher Education, Northern Illinois University, at the Lorado Taft Field Campus near Oregon, Illinois. My regular course assignments, in addition to various workshops and resident work, are Field Science and Outdoor Interpretation. In the 2 courses, technical and aesthetic aspects of nature study are combined. Outdoor Education trains teachers to use the outdoor in order to enhance their own curricula. Since Illinois is known as the Prairie State, an important part of each of my courses is prairie study. It is important to me for my students to acquire positive attitudes toward prairie.

In order to involve students without duress, positive outlooks and positive reactions must be developed. Intellectual and emotional aspects must both be reached. The cognitive (knowledge), affective (attitudes), and behavioral (action) aspects of education must all be addressed. Both knowledge and appreciation should be stressed. Together, they are more powerful than either separately. Knowledge alone can become an intellectual exercise, without meaning. Appreciation without knowledge can dwindle; at some point, enthusiasm will sag.

Direct involvement is the best teacher, and develops the greatest commitment. Both outdoor education and attitude-change theory stress direct involvement. L. B. Sharp, a pioneer in outdoor education, stated: ". . . the best way to learn is to come into contact with the things we seek to know." ("What Is Outdoor Education?" *The School Executive* 71:19-22, August, 1952) and "It is the person who sees, discovers, or explores a situation who gets the most out of it." Attitude-change theory states that involvement changes attitudes in a positive direction.

I have identified 11 necessary and helpful elements of involvement:

1. Stress both information and appreciation
2. Provide for direct experiences
3. Appeal to the aesthetic senses
4. Develop and instill appreciation
5. Appeal to the imagination
6. Appeal to the intellect
7. Provide pleasant experiences
8. Encourage a sense of community
9. Provide positive reinforcement
10. Allow cameraderie and peer pressure to exert influence
11. Be sure that good leadership is available

Following are some of my more successful experiences in involving students.

My favorite experience with grade-school children goes back to Camp Reinberg, when one of my fall teaching responsibilities was the prairie lesson and walk to the prairie "garden." The lesson usually began with a discussion. "How many of you were born in the town where you now live?" Not many. "How many of your parents were?" "Grandparents?" Fewer still, if any. "That was a long time ago. Can you imagine what this part of Illinois was like before even your grandparents were born?" We then discussed the sea of grass, how it looked, how it felt to the early pioneers, and what they might have felt if they had lived then. "Imagine yourself there." We imagined breaking through the woods as the pioneers did, and being amazed by the "sea of grass."

As we walked through the woods, excitement mounted. When we finally broke through the underbrush into the light, a hushed, "Look, there's the prairie!" could be heard, followed by "Oohs," and "Aahs." The children were so eager to see the prairie that anything would do, even an abandoned farm field.

When we actually got to the prairie, I tried to create a feeling of awe at the size of the grasses and forbs. "How might you have felt if your entire yard had been surrounded by these plants?" "Can you reach the top?" "Could your little brother or sister get lost in these grasses?" (Always a favorite with 5th and 6th grade students.) Years later, I heard from a student who remembered "Mrs. Outdoor Education and the Prairie." It stayed with them.

Involvement techniques used in this experience included the use of imagination and personal involvement (on a mental level)—an important interpretive technique.

My current field science classes explore, discover, and discuss ecosystems. Through their studies, they develop an appreciation for the diversity of systems around them. By the time we visit a prairie, students have studied 1 or 2 ecosystems on their own. They have found delight, gratification, and joy in discovery, and have known pleasure in being able to recognize different habitats. At this point, they have developed an appreciation for diversity, and can recognize the wonder in a tiny flowering plant; so they are ready for prairie.

A prairie lesson generally begins with a lecture and discussion focusing on the importance of grasslands as the heartlands and breadbaskets of the world, and their role in the development of civilization, trade, and number systems.

We discuss Illinois' prairie heritage. A map of the state 150 years ago with prairie areas marked provides an impressive visual image of recent, rapid changes. We then focus on the few remnants that are left, and the farsighted people who were instrumental in preserving and restoring what little we have now.

For our visit to a prairie, I prepare a species list of plants in the order in which we will see them. The list is not all-inclusive. People can gather and digest just so much information at one time; a long list can turn off novices. My list includes only those plants that are in bloom or have some eye-catching feature. If students ask for more information, I provide it. I make it a point never to overwhelm anyone with information. They may bring a field guide if they wish to do some investigating on their own.

I let the students ask questions; I never read the species list to them. Someone will usually ask, "Is this a coneflower?" which, of course, it is. They continue through the prairie and the species list, questioning, discovering, and feeling the rewards of positive reinforcement.

We stroll slowly through the prairie. This is a casual, relaxed experience. I believe in introducing the study of prairies through an appeal to the aesthetic senses, not through hard work. They leave with a new appreciation of the prairie and a sense of commitment to find and preserve what we still have. Many of the students from these classes have become actively involved in prairie preservation in their own schools and towns.

Involvement techniques used in this experience include an appeal to intellect, providing information, an appeal to the aesthetic senses, providing a pleasant experience, and positive reinforcement.

My classes in outdoor interpretation visit prairies on field trips. By the time they visit, they already know that the message and the technique by which it is presented are important, so they are cooperative in experiencing another technique. My favorite way to experience prairies (especially since most of them are surrounded by civilization, in full view) is to lie down and watch the grasses waving against the sky. A marvelous sense of isolation and peace results from seeing golden brown against azure blue.

We then peruse poetry books. While the class sits or lies in the grass, I read my favorite prairie poem. Class members follow with readings of their own. It is something like a Quaker meeting. During an appropriate silent time, I quietly begin to leave and the others follow.

After sharing words about the prairie, the students disperse and spend about 20-30 minutes individually developing interpretive progams for the prairie, aimed at any target group of their choosing. They then share and react to their plans.

Involvement techniques used in the experience included an appeal to aesthetic senses, use of the imagination, involvement and choice: whether and what to read, positive, immediate reinforcement, a sense of community and positive leadership.

Possibly my favorite experience in involving students in prairie work took place the summer of 1982, when Doug Wade and I took my field science class to work in Ogle County's Bicentennial Prairie. It rained until the moment we arrived, when the sun came out, and the temperature quickly soared to over 90°. We were hot, wet, and dirty from head to foot. Yet we worked with feelings of cameraderie, joining in an occasional work song led by the class spirit booster. We accepted each other's feelings when 2 of the women decided that a bird's nest was more important to save than a few square feet of prairie. Cooperation prevailed; some of us pulled weeds and cut sumac, others hauled them away to a burn pile. When individuals got bored with their jobs, they exchanged. Doug mowed the path while I cut and hauled with the class. We all left with a wonderful feeling of accomplishment at having helped preserve a small part of our heritage.

Involvement techniques used in this experience included a sense of peer pressure and cameraderie, a sense of accomplishment, a sense of belonging to and helping something bigger than one's self, and good leadership.

Perhaps this last item is the most important. A project needs a leader to make it work. If s/he is not really interested, it will show. The leader need not be what we commonly think of as charismatic, but rather someone who truly loves the project. Love creates its own charisma; enthusiasm is contagious.

This last experience was not objectively enjoyable, but the results provided enough positive reinforcement to make it subjectively enjoyable and rewarding. It seemed to be an excellent example of cognitive dissonance at work: the more unpleasant an activity, the more we have to convince ourselves of its worth to be involved in it.

Sometimes, cognitive dissonance seems to be what prairie preservation is all about.

ANALYSIS OF THE UNIVERSITY OF WISCONSIN-MADISON PRAIRIE RESTORATION PROJECT

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Abstract. The Curtis Prairie of the Arboretum, initiated between 1936 and 1941, originally consisted of 46 species separately planted in 237 plantings. Forty-six percent of the plantings were successful and 38% unsuccessful. Nine common successful species spread widely over the prairie while 9 others persisted well, but with little or no spreading between 1941 and 1982. These latter are called *documentary species* since they precisely pinpointed their planting locations for the 1982 re-survey. From these key locations, all 237 planting areas could be determined within a m or 2. From this, the plant persistence and succession in each of these plantings could be accurately documented after the 40-year interval. Some spreading species were also documentary. Starting with old farmland, this prairie has been spectacularly successful. It has been designated by the Arboretum as "the world's oldest restored prairie."

> The Arboretum's most outstanding successes in community establishment have been its prairies.
>
> GRANT COTTAM, *Management: Our first 45 years.*

INTRODUCTION

The University of Wisconsin-Madison Arboretum, established in April 1932, was described by Longenecker (1941). The best account of its history has been given by Sachse (1965). The initial development of its prairies has been briefly and informally described by Sperry (1983) and Jordan (1983), while other random aspects of their development have been published by Curtis (1952, 1959), Cottam (1962), Zimmerman (1969), Anderson (1972), Cottam (1979), and by Greene and Curtis (1953). Popular descriptions of the Arboretum at Madison and its prairies have been issued by the Arboretum Committee in undated printings as a *Guide to the Arboretum Prairies* (1970) and *The Arboretum* (1982).

Various aspects concerning the development of the prairies have also been given technical treatment in some unpublished theses at the University of Wisconsin-Madison. The most recent of these is by Blewett (1981).

This paper presents the first comprehensive account of the background and methods of the initial establishment of the Curtis Prairie (the Arboretum's subsequent Greene Prairie is not considered here), then follows with a current analysis of its successes and failures with reference to the original plantings.

THE CCC ENVIRONMENT

Shortly after the initial organization and land acquisition of the Arboretum in 1932 and 1933, national economic and political conditions made available substantial funds and manpower for conservation purposes in the form of the Civilian Conservation Corps (CCC) program. The Arboretum Committee prevailed upon the University, the State of Wisconsin, and the National Park Service (1 of the administrators of the CCC program) to establish a CCC camp on the Arboretum for its development. The Arboretum Committee, especially professors Aldo Leopold and G. Wm. Longenecker, had already proposed that the Arboretum include a replica of a "native Wisconsin prairie" of about 24 ha (60 acres) as a central feature of the new arboretum. Its central location was *not* dictated by its ecological importance, but rather because of landscape considerations which provided a low vegetation in the foreground to permit vistas where the taller forest plantings could be viewed as a mass in perspective—to negate the complaint that one "cannot see the forest because of the trees." The idea of a prairie as an entity having its own intrinsic value as a biotic community had few supporters, even on the committee itself, but neither did it have opponents, since it seemed to provide harmless open space.

Nobody knew anything about prairie replication in those days, but that did not deter Prof. Leopold from proposing to the writer that he attempt such a project:— Here are 60 acres of not-very-good old farmland, a truck and a dozen CCC enrollees with long-handled shovels. Go make a prairie out of it! With the advice and under the supervision of Leopold, ecologist and conservationist; Dr. Longenecker, horticulturalist and landscape architect; and Dr. Norman C. Fassett, taxonomic botanist, all of the University of Wisconsin, the project was started in the spring of 1936.

Scientific names in this paper follow Gleason and Cronquist (1963).

INITIAL PLANTING METHODS

The botanical materials were to be obtained from wherever available, preferably from the vicinity of Madison (mostly from Dane and Sauk Counties). Three methods of establishment were projected. The first method was the direct transplantation of prairie sod, or individual plants, when available. Not only was this source quite limited, it was found to be heavy and hard work to obtain and transplant many tons of sod to cover a very few hectares of field, even when the individual clumbs ("stools") were spaced 1-2 m apart during the planting.

The second method involved the collection of prairie seed and planting these in seed spots in the field, also at a spacing of 10-15 dm. Most of the remaining prairie in Wisconsin was limited to railway rights-of-way, roadsides, or isolated corners or rocky patches in fields. Collection was done by hand, usually in small quantities of fractions of a kg at any 1 time or place, of each species as it matured. Some of the seed heads might be broken up and the seed separated from them, depending on the type of fructification and density of the seeds in the head. Since only small quantities were involved, this work was done by hand, and sometimes required more time than its collection.

The old fields in which these seeds were planted were weedy, usually with a cover of quack grass (*Agropyron repens*) if recently plowed, or bluegrass (*Poa pratensis* or *P. compressa*) if recently pastured, and often a mixture of both. To reduce competition, the seed spots were first scalped by mattock, and the underlying soil turned over by shovel, with the bulk of the rhizomes, especially the deep rhizomes of the quack grass, removed from the soil by hand. Several seeds were sown in each spot soon after seed collection, or if collected late in the season, held over winter and sown the following spring after the soil had dried enough to be handled. Some attempts were made at tractor cultivation of the soil and rhizome removal by harrow, followed by broadcast of the seed, or by seeding in rows. This method yielded indifferent success in terms of the amount of labor required or the degree of prairie plant establishment obtained.

The third method involved the establishment of prairie nurseries for growth of collected seed, followed by transplantation of the seedlings into planting spots in the field. This method was the slowest, since it required an additional year to get the plants into the field, and required the labor of establishment and care of the nursery in addition to the preparation of the planting spots. Its advantage lay in a great increase in the number of plants obtained from only a very limited amount of seed. Here each germinating seed might be available for a planting spot, which was not practical when the seed was sown directly into the field. In some cases, nursery plants were allowed to flower and fruit in the nursery for a year or 2, to yield a relatively large amount of easily collected seed to be used for spot planting in subsequent years.

In addition to these 3 initial methods, a few experimental plantings were subsequently made, including some mixed plantings and some with no cultivation practices.

In the initial period between 1936 and 1941, some 237 plantings were made, involving 46 species of prairie plants.

CRITIQUE OF PLANTING METHODS

None of these 3 methods was recommended as a good method of prairie establishment by Curtis (1952), although a modification of the third method is today recognized as a very successful method for small prairie tracts. But it should be noted that a 1982 re-survey of these early plantings revealed an unanticipated fund of planting information which would not have been available following Curtis's recommendations for prairie restoration.

In the 1936-1940 plantings (a very few in early 1941), each species usually was planted in spots in a discrete area, the number varying from as few as 10 up to 10,000 spots per planting, determined by the amount of material available at the time. The location of each planting was selected by topographic considerations of species preference and by the location of the previous plantings. It was deemed advisable that once an area was planted, the crew should be kept off the planting area to prevent trampling. Such trampling occurred in the first planting in 1936 when watering of the sod transplants was attempted to alleviate the 100°F drought conditions which prevailed at that time. The trampling affected the plantings as severely as the temperatures and drought, even though an abortive effort was made to keep the inexperienced crew off the planting spots.

Furthermore, since prairie planting is relatively slow due to the close spacing of the planting spots (as contrasted with shrub spacing at 2-5 m intervals and tree spacing at 7-10 m intervals), there was an effort to spread out the plantings over an area extensively rather than intensively. This was done to get prairie plants established in as short a time as materials and labor permitted. (The CCC was a "make-work" program.) It was hoped that once established the various species would spread into adjacent plantings to produce a homogeneous mixture of prairie plants.

As additional planting material became available, however, subsequent plantings of the same species would be removed from earlier plantings to provide a series of separate centers of dispersal across the prairie area, at the same time providing for planting in different soils and under a variety of climatic conditions in different seasons in different years. If 1 planting should fail, the species would have a chance of success in a different soil in another season. At that time, nothing was known about the arboretum soil except its wet and dry locations. Soil surveys of the area were dreams for the future. In those post-Dust-Bowl years, even the potentially "wet" soils were too dry for success, and there was a logical tendency to place many of the mesic species onto lower soils with the hope that they would obtain enough moisture for survival. The immediate availability of CCC labor did not permit deferral of prairie planting a year or 2 until moisture conditions were more favorable.

Since the plantings were mostly limited to 1 species per planting, subsequent observations quickly revealed when and if a species invaded areas outside its own planting area and at the same time determined whether such a planting area was invaded by another species, and how rapidly this invasion occurred. Also, since it was known how many seed (or planting) spots there were within a planting, the survival and reproduction rates within the planting area could be determined. From this, an estimate might be made of the time required for a restored prairie to become stabilized, if stability is ever actually attained. While this method should require a longer time span for a prairie to attain homogeneity, observation of native prairies indicates that homogeneity is scarcely a characteristic of prairies under any conditions. Too many variables prevail for this eventuality, quite apart from the fact that modern prairies are missing such factors as the larger grazing ungulates and their predators, and are subject to invasion by many non-native weeds.

POST-CCC METHODS

Following closure of the CCC camp in 1941 as a result of World War II exigencies, the Arboretum remained intact and operative under a succession of administrators and changes in staff as well as composition of the Arboretum Committee. While no major changes of policy were adopted as a result of these shifts, differences of interests as well as variations in financial support have had their effects on development of the area. So also has the growth of the city of Madison, especially the construction of a major arterial highway (called the Beltline) along the southern edge of the Arboretum, which has created erosional, drainage and pollution problems.

University students and staff continually find the Arboretum an excellent field laboratory for teaching and research problems, including various planting and seeding projects on the prairie, as well as a variety of management techniques. Perhaps the most significant of these has been the adoption of regular periodic burning of various portions of the prairie starting early in the 1950s.

These variants of management have been more or less regularly documented, frequently with limited follow-up studies to determine their effectiveness. The same is true for those unplanned events, such as unplanned fires or seasonal climatic extremes. One of the biggest changes in the Curtis Prairie was the construction in about 1969 of a big siltation pond along its central southern edge to control siltation deposits from suburban lands to the south, arriving through a major highway culvert.

LIMITATIONS OF VEGETATION ANALYSIS

No attempt is being made here to summarize all the developments over the post-CCC 40-year period (1941-1981) nor to review the documentary records of vegetational changes resulting from them. This would be a major project in itself which may never be accomplished due to lack of funds and personnel. For the present study it is being assumed that all prairies have always had both cyclic and random environmental changes, some of major proportions, which have affected the plant cover and left the prairie with unexplained unique aspects which the then current investigator duly records in his notes.

A complete re-survey of the initial plantings was made by this writer following World War II in the spring (March-May) and summer (August) of 1946, and while these notes were kept with those of the initial plantings, no work was published to compare these with the notes made during the 1936-1941 development. They are used, however, for the present study whenever they show any intermediate developments of interest, and are included in the tabular summarization in the unpublished appendix to this paper.

No further re-survey of these plantings was made until the period of 22-29 June 1982 when this writer located and checked each of the 237 planting areas established during the 1936-1941 period. These plantings were segregated into 72 specific categories with 1-13 replicate plantings in each category. These categories were based on the primary species and on the type of planting; i.e. seed spots, sod (or wild) transplants, and transplants of nursery-grown plants. Survival rates were determined for each planting based on the percentage of planting spots that contained plants of the indicated species (or equivalents when other planting methods were used). These survival rates are reliable to the extent that each planting consisted of an average of several hundred spots and the larger plantings, of thousands (Table 1).

TABLE 1. The primary categories of planting success.

% OF PLANTING SPOTS CONTAINING PLANTS	CATEGORY CLASSIFICATION	NO. OF PLANTINGS	% OF TOTAL PLANTINGS
Successful plantings			54.6
95 to 100	Very good (and excellent)	53	26.8
65 to 95	Good	36	18.2
35 to 65	Fair	19	9.6
Unsuccessful plantings			45.4
5 to 35	Poor	19	9.6
Present to 5	Very poor	4	2.0
None found	Zero	67	33.8
Totals		198	100.0

TABLE 2. The survival of prairie grasses.

Species	Planting method	Success
Successful species		
Andropogon gerardii	Sod planting	Very good
	Seeds	Good
Sorghastrum nutans	Sod planting	Very good
	Seeds	Very good
Spartina pectinata	Sod planting	Very good
	Seeds	Zero
Unsuccessful species		
Andropogon scoparius	Seeds	Poor (but germination was very good)
Aristida intermedia	Seeds	Zero (germination fair)
Bouteloua curtipendula	Seeds	Zero (germination fair)
Bouteloua hirsuta	Seeds	Zero (germination fair)
Elymus canadensis	Seeds	Zero (first year growth was very good)
Koeleria cristata	Seeds	Zero (germination was very good)
	Transplants	Zero (first year survival was fair)
Panicum virgatum	Seeds	Zero
Sporobolus asper	Seeds	Zero (germination very good)
Sporobolus cryptandrus	Seeds	Zero (germination zero)
	Transplants	Very poor
Stipa spartea	Seeds	Very poor (germination was fair)
	Transplants	Poor

REMOVED PLANTINGS

Between 1941 and the re-survey of 1982, 39 plantings (16.4% of the total of 237) were removed from consideration due to historical developments. Twenty-five (10.5%) were in the area covered by the siltation pond or by the 15-foot-high berm containing it on the east, north and west sides of the pond. The remaining 14 (5.9%) were in peripheral areas around the prairie which were subsequently planted to a forest cover, to horticultural plantings, or converted to a 5 m-wide fire lane constructed between the prairie and the forest plantings. Fourteen other prairie plantings were also partially destroyed by these developments, but as long as a portion of each area is still retained as prairie it is listed as a separate, albeit a reduced and smaller, planting area.

STATISTICAL DATA

Since it is not feasible to include here all of the statistical details of these plantings and re-surveys, it should be noted that the original notes and maps and complete statistical tabulations of the analysis are on file in the Director's office at the Arboretum (The University of Wisconsin-Madison Arboretum, 1207 Seminole Highway, Madison, Wisconsin 53711. Telephone 608-262-2746) and may be examined upon request by parties having use for this information.

SURVIVAL OF PRAIRIE PLANTINGS AND SPECIES

The success of each of the plantings was measured by the percentage of the planted spots containing plants of the primary species at the time of the re-survey. These ranged from excellent (for 100% of the spots) to zero (no plants found), with 6 categories recognized as shown in Table 1. Plantings with category ratings of very good, good or fair were considered successful, while those with ratings poor, very poor or zero were listed as unsuccessful.

Of the 198 plantings still extant for the 1982 re-survey, 108 (55%) may be considered as successful, and 90 (45%) as unsuccessful. A pronounced difference in survival was noted between the grasses (Table 2) and the forbs (Table 3) as summarized in Table 4.

Commentary on Species Persistence

It was assumed during the initial years that not all plantings would be successful. The whole arboretum project was initiated on a substantial amount of faith! Which of the trials would be successful remained to be determined.

It was known, of course, that much of the Curtis Prairie environment was not ideal for many of the prairie species, but when seed (or plants) were on hand, they were used with the hope that some of them might survive. Hence there were a few small plantings (some with as few as 10 spots) for seeds that were on hand, for which no repeat plantings were attempted, e.g. *Aselepias incarnata, Castilleja sessiliflora, Sisyrinchium campestre, Lobelia cardinalis.* Likewise, some of the smaller praire grasses normally occur on lighter, drier soils, but when such were not available (at that time) on the Arboretum, they were planted on heavier soils. It was hoped that some of them would survive if not flourish. This was actually the case only with *Stipa spartea* and *Andropogon scoparius* (Table 3).

The failure of 28% of the forb species to become established is about what might have been anticipated, but the failure of 8 (61%) of the grass species was substantially greater than expected. Perhaps it is natural to be disappointed with these non-persisting experimental species, but we still have ample cause for elation concerning the large number of persisting species, some of them spectacularly successful.

The highly successful species can be divided into 2 general groups—those which have persisted for many (more than 40) years, growing, flowering and fruiting well, but not spreading significantly from their original planting areas, and those which have not only grown very well, but have spread, either by seeds or by rhizomes or both, far beyond the boundaries of their original planting areas. Plants in the latter group, those now widely spread over much of the Curtis Prairie area since the original plantings, include *Andropogon gerardii* and *Sorghastrum nutans* among the upland grasses and *Spartina pectinata* in the wet prairies, and for the upland forbs, *Baptisia leucantha, Echinacea purpurea, Eryngium yuccifolium, Liatris aspera, Ratibida pinnata* and *Silphium terebinthinaceum,* among others. No wetland forbs were abundant.

Documentary Species

Noteworthy among the poorly-spreading persisters are *Amorpha canescens, Baptisia leucophaea, Ceanothus americanus, Helianthus laetiflorus, Phlox pilosa, Rosa carolina, Silphium integrifolium, S. laciniatum* and *Stipa spartea.*

It is this group which proved to be the most useful in documenting the 1982 re-survey. Although the original plantings had all been marked by labeled stakes at the time of establishment and at the time of the mapping in 1939 and 1940, these stakes had long since disappeared from the combined impact of fungi, termites, prairie ecologists' boots, and fire. It was therefore necessary to relocate the original planting areas from the maps by using bearing and distance measurements from available (but scarce) landmarks. Although this method of relocating the planting areas was reasonably reliable, it was not effective in precisely pinpointing the original planting boundaries.

The Ceanothus *plantings.* It was the *Ceanothus* which first provided the clue to the exact planting locations. This is a relatively conspicuous shrubby plant (technically not a forb) which showed up easily in the herbaceous prairie cover. Since it had survived very well but had not spread significantly, once these plants had been found, it was possible to determine exactly (within 1 m) the original boundaries of the planting. There were still the same number of planting spots distributed in the same planting pattern as there had been in the original seed planting 42 years earlier! Hence the *Ceanothus* is designated as a *documentary species* in pinpointing its original location. There were 3 *Ceanothus* plantings in different parts of the Curtis Prairie, planted respectively on 7 October 1938, 14 July 1939, and 9 October 1940. A few younger plants have since become self-seeded outside of the original boundaries and growing well, but not enough at this time to obscure the original planting limits.

TABLE 3. The survival of prairie forbs.

SPECIES	PLANTING METHOD	SUCCESS
Successful species		
Amorpha canescens	Seeds	Good (seed germination was *very* slow)
Aster laevis	Seeds	Fair (variable)
	Wild transplants	Fair (variable)
Baptisia leucantha	Seeds	Very good
Baptisia leucophaea	Seeds	Good (seed germination slow)
Ceanothus americanus	Seeds	Very good (seed germination slow)
Coreopsis palmata	Seeds	Very good (seed germination slow)
Echinacea purpurea	Seeds	Very good
	Transplants	Very good
Eryngium yuccifolium	Seeds	Very good
	Wild transplants	Very good
Helianthus laetiflorus	Seeds	Good (somewhat variable)
Lespedeza capitata	Seeds	Good (somewhat variable)
Liatris aspera	Seeds	Good (development slow)
	Transplants	Good (development slow)
Liatris cylindracea	Seeds	Good (results uncertain)
Liatris pycnostachya	Seeds	Fair
	Transplants	Very good
Phlox pilosa	Seeds	Fair (development slow)
Pycnanthemum flexuosum	Seeds	Good
Ratibida pinnata	Seeds	Good
	Transplants	Good
Rosa carolina	Wild	Good (development slow)
Silphium integrifolium	Seeds	Very good
	Transplants	Good
Silphium laciniatum	Seeds	Good
	Transplants	Very good
Silphium terebinthinaceum	Seeds	Very good
	Wild transplants	Very good
	Transplants	Very good
Solidago rigida	Seeds	Fair
	Transplants	Fair
Tradescantia ohiensis	Seeds	Fair
	Transplants	Zero
Unsuccessful Species		
Asclepias incarnata	Seeds	Zero (trial poor)
Asclepias tubersoa	Seeds	Zero (seed germination was very good)
	Transplants	Poor (but plants did not persist)
Asclepias verticillata	Transplants	Zero (initially good for several years, but plants did not persist)
Astragalus canadensis	Seeds	Zero (seed germination poor—did not persist)
Castilleja sessiliflora	Seeds	Zero (trial poor)
Hieracium longipilum	Seeds	Zero
Lobelia cardinalis	Transplants	Zero (trial poor)
Petalostemum candidum	Seeds	Zero
Petalostemum purpureum	Seeds	Zero
	Transplants	Zero (initial growth poor)
Rudbeckia hirta	Transplants	Poor (growth good in the wild)
Sisyrinchium campestre	Seeds	Poor (growth fair in the wild)

Other documentary species. Once this was noted for the *Ceanothus*, the same phenomenon was detected for other species in this group with approximately the same degree of certainty. This was true even for species with a relatively low incidence of persistence. For example, a planting of *Phlox pilosa* had been placed adjacent to a planting of *Tradescantia ohiensis*. When this area was examined in 1982 when both of these species were in flower, the scattered pink flowers of the Phlox, which had a persistence rating of "poor", stood out clearly on the north side of the presumed planting boundary, contrasting with the scatterred blue of the spiderwort, also with a "poor" persistence rating, adjacent to it on the south side of the boundary. This was more than 40 years after these species had been planted.

Even the *Stipa spartea*, which was nearly absent from the Curtis Prairie, could be found with a "fair" abundance when in "flower," only within the area where it had been planted on 18 August 1938 in seed spots on some moderately well-drained soil.

With enough of these "key" planting areas scattered around the prairie, it was possible to locate within narrow limits each of the 237 planting areas of the 1936-1941 plan-

TABLE 4. Comparative success of grass and forb species.

	GRASSES		FORBS	
CATEGORY	No.	%	No.	%
Very good	3	23.1	8	25.0
Good	0	—	9	28.1
Fair	0	—	3	9.4
	3	23.1	20	62.5
Poor	1	7.6	3	9.4
Very poor	1	7.6	0	—
Zero	8	61.5	9	28.1
Totals	10	76.7	12	37.5

tings, including those for which no germination or establishment had been previously observed. The degree of stability noted for these prairie species should not be considered a general characteristic of the species. In other edaphic or climatic environments or under other management practices these species might not show this same stability.

On the other hand, some species with widely spreading habits showed considerable stability in distribution patterns. *Baptisia leucantha* and *Eryngium yuccifolium* have become so abundant and widespread on the Curtis Prairie that there was no hope of detecting from their present distribution the restricted limits of the original plantings. *Silphium terebinthinaceum* was likewise very abundant and widespread in 1982, but when the known planting areas were examined it was found that the density of this species within the area from which it had spread was 2 or 3 times greater than it was just outside of the boundaries of those areas into which it had invaded. Thus it was still easy, at least in the mid-June stage of growth, to locate the original planting boundaries. This same phenomenon was also evident for *Echinacea purpurea* and *Silphium integrifolium.*

Even *Andropogon gerardii* showed this characteristic. The clumps of sod placed in the quack grass-covered soil in 1936 still showed the same old clumps with the same spacing in 1982 in spite of the extensive spreading this species has shown since that time. Although *spreading* big bluestem shows the bunchgrass character of the species, the spreading plants do not show the regularity and uniform intervals of spacing as that resulting from the CCC crew planting. This distribution pattern has been remarked by many observers of this planting over the intervening 46 years, and it still remains true.

Other species still showing distribution patterns exhibiting their original planting boundaries or localities are *Aster laevis, Baptisia leucophaea, Coreopsis palmata, Lespedeza capitata, Liatris pycnostachya, Pycnanthemum flexuosum, Solidago rigida,* and *Spartina pectinata.* It is probable that other species might show this same survival pattern, but none other was noted with certainty during the 1982 survey.

Failures in Planting Persistence

Even when a species has had successful plantings, certain plantings of the same species have shown poor or even zero persistence. In most such cases, the cause was poor selection of planting site. For example, a planting of *Eryngium yuccifolium* placed in a low area on 13 October, 1937, following the very dry years of 1934, 1935 and 1936, had very good growth in 1938, and continued to show good survival as late as 1946. By 1982, however, following a period of above average rainfall, it showed zero persistence in an area covered with water 2-5 cm deep. This also happened with *Solidago rigida* (2 plantings), *Silphium integrifolium, Liatris pycnostachya, Aster laevis, Tradescantia ohiensis* (2 plantings), and perhaps others, all in areas much too wet. Good initial survival did not necessarily ensure good permanent persistence. Other cases of lack of persistence could be attributed to severe machine disturbance during construction of the siltation pond, or to heavy erosion or silt deposition along drainageways prior to erosion control measures.

On the other hand, *Elymus canadensis* in 5 plantings showed very good survival in the first year after planting but each dropped to zero prior to the 1946 survey. This has been found true for this species in plantings elsewhere as well (author's experience and personal communications). Eight plantings of *Asclepias verticillata* showed a similar pattern. At 1 time it appeared that this species might become a rather pestiferous weed on the Arboretum, but it seems to have disappeared entirely in recent years. Both of these appear to be disturbance species, and may well have depended upon the bison or other grazers to keep disturbance habitats available for them in the prairies.

The reverse seemed to be true for *Amorpha canescens.* For this species (planted in 1938 and 1940) the initial observations were recorded as zero and the 1946 survey likewise showed zero. Yet in 1982 both plantings showed good growth with abrupt boundaries coinciding exactly with the map locations. As with various other legumes, the germination of this species was apparently delayed a number of years, possibly until more or less regular burning was initiated in the early 1950s. No spreading of these plants was noted in the 1982 survey. Other plantings showing a parallel response were *Rosa carolina* (2 plantings), *Aster laevis* (1 planting), and *Ceanothus americanus* (2 plantings). The specific factors responsible for these delays remain to be determined.

Termination of a Persistence Pattern

Baptisia leucantha generally showed a poor or very poor "survival" in the initial years, but by 1946 these plantings were showing good to very good growth but with very little spreading. These remained in good condition, but mostly confined to their planting areas as documentary species for the next 25 or 30 years. Then, very unobtrusively (about 1970), they began a relatively rapid spread far beyond their planting boundaries to cover large areas of the Curtis Prairie in a rather spectacular display. No good explanations for this have yet been advanced in spite of varied environmental factors which have been postulated. We still know too little about soil biodynamics.

Baptisia leucophaea, also present on the Arboretum in much smaller numbers, has shown no such tendency, and the 1 successful plot planted in 1940 meekly remains in a very healthy but stable condition with no indication of spreading.

ADDITIONAL EXPERIMENTAL PLANTINGS

Four other categories of planting areas were established at this same time: (1) Natural Populations groups, (2) Mixed Broadcast Seeding, (3) Mixed Prairie Transplants, and (4) Unplanted Prairie Control Areas.

The first of these consisted of small populations of bluestem, rose, and brown-eyed susans found persisting in the old fields or pastures. These were preserved intact, usually in a disturbed or weedy condition, instead of being replanted. One of the patches of *Andropogon gerardii* in a low, rather muddy area eventually developed into a fairly good patch of wet *Andropogon-Spartina* prairie, while another similar peripheral area was allowed to become woody and is now a part of a swamp forest community containing no prairie plants. The difference can be attributed directly to differences in environmental management. No replanting was done.

Three patches of *Rosa carolina* were converted (in part) into horticultural areas or into fire lanes, or have become shrubby patches of *Rhus* and *Cornus* within the prairie, but 2 still persist as good patches of the rose. The 2 patches of *Rudbeckia hirta* appeared to have an evanescent persistence, spreading opportunistically into other areas or being invaded extensively by various more aggressive species.

Category 2, a single planting consisting of mixed broadcast seeding, was in an area of undisturbed bluegrass and quack grass sod onto which miscellaneous surplus seed of various prairie species (*Phlox, Liatris, Lespedeza, Eryngium, Aster,* etc.) were broadcast over the sod with no further attention other than the normal prairie maintenance (burning, etc.). The initial observations were rated zero, but by 1946 the bluegrass and quack grass sod contained a fair scattering of *Lespedeza, Ratibida, Echinacea, Eryngium,* and the silphiums, either from the broadcast seeds or by invasion from adjacent plantings. By 1982 the area was rated good bluestem prairie, rather well covered by the tall prairie grasses (including some *Andropogon scoparius*) and more than a dozen species of widely spread prairie forbs, but still containing significant amounts of such weedy species as *Melilotus, Pastinaca, Erigeron, Asparagus,* etc. It seems that, given enough time with appropriate management, one could eventually establish a prairie with no planting at all as long as the necessary seeds were made available.

Category 3, the Mixed Prairie Transplants, was similar, using planted material instead of seeds, and placing the transplants into scalped planting spots. There were 3 of these plantings mainly using surplus nursery-grown stock. These trials were rated fair to very good, producing a weedy to very good prairie. More labor is required, of course, than with the seed broadcast method, but these plots were rated good by 1946, thus speeding up the rate of prairie establishment by 10 to 40 years. This method is to be recommended above that of the single-species method reported here providing, of course, that seed and nursery material is available for its planting.

Category 4, listed here as the Prairie Control Areas, consisted of doing nothing beyound prairie management and periodic observations, but required that other prairie plantings or plots be present in the vicinity to provide seed. Also required are planted areas with which these controls could be compared. As would be expected, these areas were rated (with respect to the prairie plants present in them), initially as zero, very poor or poor, and from very poor to fair by 1946. But of these 6 Prairie Control Areas, by 1982 1 had been removed (now converted into pine forest), 1 was fair (part of it covered by the siltation pond berm and the remainder heavily damaged during the pond construction), 1 was good, but in an area made weedy or *Rhus*-covered by an erosion and siltation drainageway, 2 were rated very good and 1 excellent—a beautiful prairie area. One of those rated very good was a wet prairie area and 1 was a well-drained dry area having a 10% runoff slope, hence with scattered weedy species. Conclusion: Control areas can become good prairie in time, given good management and good near-by prairie.

SUMMARY

A. A very creditable replication of a tallgrass prairie can be restored on old farmland, given enough time and appropriate management.

B. Although more efficient methods of prairie restoration may be possible, the segregation of plantings into discrete species-planting areas permits an evaluation of rates of species establishment and invasion not otherwise available.

C. Of all the 237 (1936-1941) plantings established, 108 (45.6%) are considered as successful and 90 (38%) as successful. (The remaining 16.4% were removed for historical reasons.)

D. Three species of grasses and 22 species of forbs are included in the list of successful plantings. Ten grasses and 11 forbs are listed among the unsuccessful plantings.

E. Among the highly successful, 9 species have spread to cover relatively large areas of the Curtis Prairie. These include *Andropogon gerardii* and species of *Sorghastrum, Spartina, Baptisia, Echinacea, Eryngium, Liatris, Ratibida* and *Silphium.*

F. The non-spreading but otherwise well-established persisting species were of significant interest, hence designated as *documentary species,* since these still occupied the same planting areas in which they were originally placed, often still in the original planting spots. These included species of *Amorpha, Baptisia, Ceanothus, Helianthus, Phlox, Rosa, Silphium* and *Stipa.*

G. Even in some widely spreading prairie species, the density of these plants remained much greater (often 2 to 3 times more dense) within the boundaries of their original planting areas than in invaded adjacent areas outside of the original planting. These, also designated as documentary species, included *Silphium terebinthinaceum, S. integrifolium* and *Echinacea purpurea.*

H. From the known locations of at least 29 widely distributed plantings of the above 2 groups of documentary species, plus the planting maps and a very few available topographic landmarks, it was possible to locate within narrow limits of 1-2 meters all of the 237 original plantings.

I. From this, it has been possible to determine vegetational succession over a 41-46 year period which has occurred on each of the 198 still-extant plantings.

J. The 1946 survey of these plantings provides persistence information at a critical stage in this succession.

K. *Baptisia leucantha* exhibited a unique phenomenon by remaining as a documentary species ("just sitting there") for some 25 or 30 years following its planting; then about 1970 starting an unobtrusive but rapid spread far outside its original plantings to cover extensive parts of the Curtis Prairie.

L. The Broadcast Seeding and Mixed Prairie Transplants attempts and the establishment of the Prairie Control areas all provide support for Curtis's (1952) recommendations concerning effective methods of prairie restoration.

M. Many of the perennial forbs and grasses have a long life (now known to be more than 40 years) with a stability and tenacity under field (wild) conditions which is equal to that more commonly associated with shrubs and trees,

and finally . . .

N. The writer in 1938 quoted J. E. Weaver as saying that a prairie, once destroyed, will require a thousand years to be restored (i.e., to a completely natural condition). The present study, covering a period of more than 40 years on the Curtis Prairie, lends support to this statement.

O. Its eventual confirmation required that a start be made some time, and it mandated the vision and leadership of such men as Aldo Leopold, Bill Longenecker, and other members of their committee, early in the 1930s, to initiate such a project (with support from the National Park Service).

P. This allows the present Arboretum administration to designate the Curtis Prairie as "The World's Oldest Restored Prairie."

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INTRODUCTION OF SELECTED PRAIRIE FORBS INTO AN ESTABLISHED TALLGRASS PRAIRIE RESTORATION

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Abstract. Under current prairie restoration practices, grasses dominate many plantings to a greater extent than in natural prairies. Many things contribute to this phenomenon, such as the fact that prairie grasses are often in much greater supply and cost less than forbs. Twenty-six selected forb species were introduced in the established *Sorghastrum nutans-Andropogon gerardii* prairie sod at the Fermilab Prairie restoration site, Batavia, Illinois, in the spring of 1981. Selection of forbs was determined by available seed and the characteristics of the experimental environment. The purpose of the study is to determine which of a series of planting techniques is most successful in enriching the composition of the Fermilab Prairie. The 9 techniques are as follows: (1) a control, (2) planting forb seeds after a burn, (3) planting forb seedlings after a burn, (4) planting forb seeds after a burn and mowing, (5) planting forb seedlings after a burn and mowing, (6) planting forb seeds after a burn and soil scarification, (7) planting forb seedlings after a burn and soil scarificaiton, (8) planting forb seeds after a burn and removing sod plugs, (9) planting forb seedlings after a burn and removing sod plugs. Preliminary results indicate that the seedling treatments are more successful initially. The most successful treatment was the scarify/seedling, with the least successful sod removal/seedling.

INTRODUCTION

The purpose of this study is to determine which of a series of planting techniques is most successful in introducing individual forb species to the Fermilab Prairie Restoration Project, currently dominated by prairie grasses. To achieve the long-range goal of having the restoration mimic species composition of presettlement prairie communities, a forb enrichment program is necessary. The planting techniques studied include introducing seed and seedlings of forbs into the existing prairie grass-dominated sod after the following treatments: (1) a burn, (2) a burn followed by mowing, (3) a burn followed by soil scarification, and (4) a burn

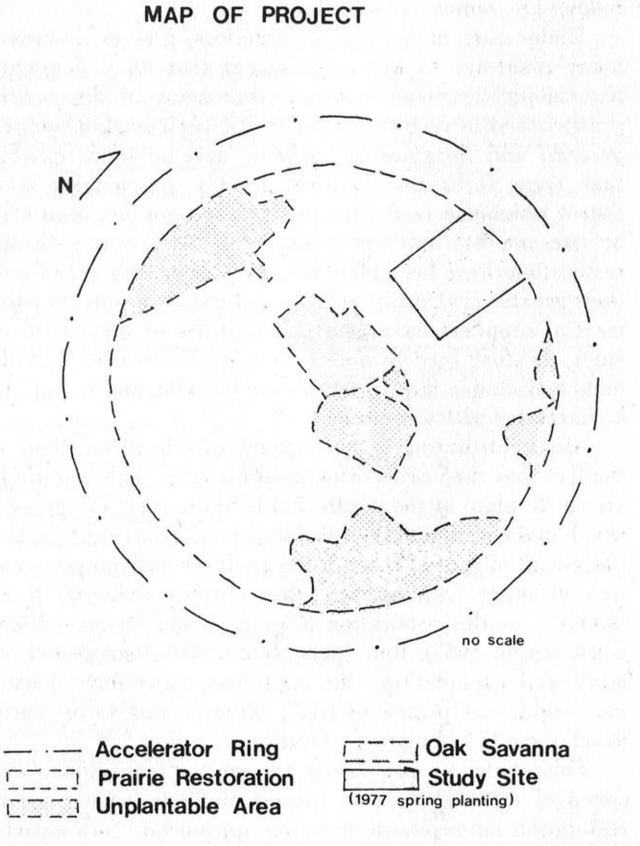

FIG. 1. Location of study area within the Fermilab Prairie Restoration.

TABLE 1. Species found in the 1977 Spring Planting Area.

	STATUS	
SPECIES	1980	1982
Andropogon gerardii	A*	A
Apocynum sibiricum	U	—
Asclepias incarnata	C	—
Aster novea-angliae	—	R
Baptisia leucantha	—	R
Coreopsis tripteris	—	R
Eryngium yuccifolium	C	—
Helianthus grosseserratus	U	—
Lobelia spicata	—	R
Lycopus americanus	U	—
Lythrum alatum	U	—
Panicum virgatum	U	C
Petalostemum candidum	—	R
Petalostemum purpureum	—	R
Ratibida pinnata	U	C
Silphium integrifolium	U	C
Silphium laciniatum	C	C
Silphium terebinthinaceum	U	C
Solidago rigida	—	R
Sorghastrum nutans	A	A
Vernonia fasciculata	R	C

* *A*, Abundant; *C*, Common; *U*, Uncommon; *R*, Rare; —, Not Found

followed by removal of sod plugs.

Under current restoration practices, grasses dominate many plantings to a greater extent than they dominate natural prairies. One reason is that many of the prairie grasses used in restoration plantings, such as *Andropogon gerardii* and *Sorghastrum nutans*, develop more quickly than many forbs and, in turn, develop a renewable seed source which can seed into open areas where forb seed may be present, but not yet germinated. Also, many recent restorations have been planted heavily to grasses because of their greater availability relative to forbs. Not only do commercial suppliers have greater quantities of grass seed in stock, but forb seed is more expensive. Grass seed is easily hand collected in large quantities in the wild, and it also can be harvested with a combine.

Also contributing to grass dominance in restorations is the fact that seed drills often used for large-scale plantings are set to plant at the depth that is optimal for the grasses which make up the bulk of the seed mix. This results in the placement of seed at a depth too great for optimal germination of many forb species, thus further reducing their numbers in the restoration (Clements and Weaver 1924, Christiansen 1967). Betz (pers. comm. 1982) suggested an additional explanation—the idea that many forb species may require a "prairie matrix", often lacking in the early development of a prairie restoration.

This study, by comparing the cost, effectiveness, and speed of establishment of several methods, should assist restoration managers in choosing appropriate forb enrichment techniques.

METHODS AND MATERIALS

Description of the Study Site. Fermilab is at Batavia, Illinois, approximately 30 mi west of Chicago in DuPage and Kane Counties. The restoration is located on 617 acres located inside the accelerator ring (Fig. 1). Winds are prevailing from the south-southwest to north-northeast. The soil type is Wauconda silt loam (a prairie soil) on a slope of 0 to 1.0%. Prior to the restoration, the land was in old field succession with the restoration process beginning in the spring of 1975.

The 1977 Spring Planting (location of experiment) was accomplished by the use of a Nesbit seed drill moving in an east-west direction. The planting rate was 30 pounds/acre (Donaldson 1981). The rows left by the drill are an evident character of this portion of the restoration. Thirteen different prairie species were found in 1980 of which 10 are forbs. Five species present in 1980 were absent in 1982; 8 species are apparently new to the planting in 1982 (Table 1).

Formulation of Forb Species Mix. As one of the goals of this project is to create a prairie with a species composition similar to that of presettlement communities, which forb species to use was decided by comparing a list of available seed with lists of prevalent species for wet-mesic and mesic prairies in *The Vegetation of Wisconsin* (Curtis 1959). Although these lists are less applicable to Illinois than Wisconsin, they probably provide a good indication of the composition of the original prairies. Using this method, 26 species were chosen (Table 2).

To mimic relative abundances of forb species in the presettlement prairies, prevalent species lists (Curtis 1959) were also used as a guide for determining the planting proportions of the forbs. For each species included, a relative frequency statistic was calculated and used to determine the percentage of the total planting made up of that species. Relative frequency was calculated by dividing the average frequency for a species (Curtis 1959) by the sum of the average frequencies for all 26 species in the mix. The number of seedlings or seeds used was determined by multiplying that relative frequency by the total number of seeds or seedlings desired (Table 2). A forb density of 25 plants per square meter was chosen arbitrarily as the desired target. The relative frequency statistic is probably a poor representation of relative abundances but it is the best quantitative information available.

Plot Layout. The experimental design used for this study was a randomized block design consisting of 36 plots 4.0 × 4.0m plots with a 1.0-m

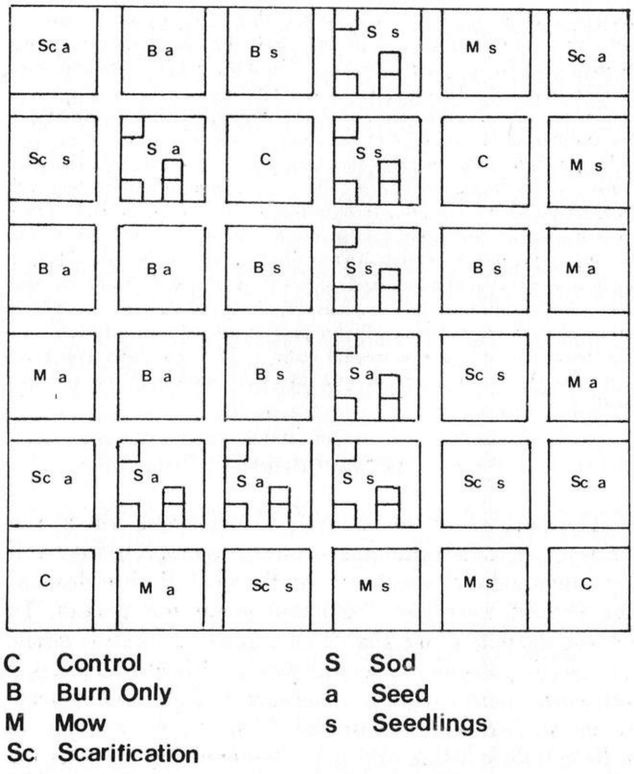

FIG. 2. Diagram of the experimental plots.

TABLE 2. Species selection and rates.

SPECIES	AVER. FREQ.*	REL. FREQ.	% OF PLANTS	PLANTS PER PLOT	NO. OF SEEDS
Allium cernuum	.01	.0026	0.3	1	36
Amorpha canescens	.32	.0836	8.4	34	1224
Anemone cylindrica	.05	.0131	1.3	5	180
*Baptisia leucantha*** ***	.01	.0026	0.3	1	36
Coreopsis palmata	.34	.0888	8.9	36	1296
*Desmodium canadense***	.05	.0131	1.3	5	180
Echinacea pallida	.01	.0026	0.3	1	36
Eryngium yuccifolium	.21	.0548	5.5	22	792
Lespedeza capitata	.18	.0470	4.7	19	684
Liatris aspera	.18	.0470	4.7	19	684
Monarda fistulosa	.22	.0574	5.7	23	828
Oxypolis rigidior	.04	.0104	1.0	4	144
Parthenium integrifolium	.01	.0026	0.3	1	36
Penstemon digitalis	.01	.0026	0.3	1	36
*Petalostemum purpureum***	.07	.0183	1.8	7	252
Potentilla arguta	.13	.0339	3.4	14	504
Ratibida pinnata	.48	.1253	12.5	50	1800
Rudbeckia hirta	.24	.0621	6.3	25	900
Rudbeckia subtomentosa	.01	.0026	0.3	1	36
Silphium integrifolium	.15	.0392	3.9	16	576
Silphium laciniatum	.08	.0209	2.1	8	288
Silphium terebinthinaceum	.31	.0809	8.1	32	1152
Thalictrum dasycarpum	.16	.0418	4.2	17	612
Tradescantia ohiensis	.31	.0809	8.1	32	1152
Veronicastrum virginicum	.17	.0444	4.4	18	648
Zizia aurea	.08	.0209	2.1	8	288

*From Curtis (1959)
**Inoculated
***Scarified

buffer zone between each plot (Fig. 2). There were 4 replicates of each treatment. The plots were located in an area that was visually relatively homogeneous in slope and vegetation.

Seed Treatment. Seed was hand collected within a 50-mi radius of the study site during the fall of 1980. The seed was cold dry stratified for 3 months. The appropriate species were scarified and inoculated (Table 2).

Ground Treatment. All experimental plots were planted to seeds or seedlings following 1 of the 4 ground-preparation treatments. All plots were burned in early April 1981 during the annual burning of the entire restoration. Therefore, the burn was a pre-treatment for all plots.

The first treatment involved the burn only. Introduction of seeds or seedlings followed.

The second treatment involved repeated mowing of the established prairie grasses. The first mowing took place 21 May 1981. The mowing was done with a rotary blade at a height of about 1 inch above the soil surface. A second mowing occurred on 1 July 1981 at a height of about 4 inches. Clippings were not removed.

The third treatment consisted of a scarification of the soil surface. The first tilling, with a hand-operated rototiller was done 21 May 1981 to the 4 seed quadrants. A second treatment, of the remaining 4 quadrants, 1 July 1981 used a rear-mounted tiller on a cub-cadet tractor. Tilling depth was ½ to 1 inch.

The fourth treatment involved removal of sod plugs. This was accomplished using a sod spade to remove 4 randomly placed 1 × 1m quadrats within the appropriate plots. A depth of approximately ½ inch was removed from the surface. Plants and soil were removed at this uniform depth. The 4 seed plots were treated 22 May 1981 and the 4 seedling plots 1 and 2 July 1981.

Seed and Seedling Planting. The pre-determined seed mix was hand spread over the appropriate plots 22 May 1981.

Seelings were started 25 May 1981 in a greenhouse and grown in wooden flats until the plants obtained 2 sets of true leaves. They were then removed to a lathe house for hardening and after about a week were transplanted directly into the designated plots. Depending on the species, planting occurred between 2 July and 30 July 1981.

The seedling establishment did not proceed as originally planned. Of the initial 26 species, 13 either did not germinate at all or germinated at such a low rate that there were not enough seedlings to give the desired total. Table 3 lists the seedlings that were actually planted.

Field Data Collection. Field data were collected in early October 1981 and from 30 June to 6 July 1982 and had been collected again in October 1982. Data include counts of the forb species present in each plot as well as information on numbers of flowering individuals.

TABLE 3. Seedlings planted.

SPECIES	NO. PLANTED TREATMENT	NO. PLANTED SOD REMOVAL
Anemone cylindrica	12	4
Baptisia leucantha	4	4
Coreopsis palmata	40	8
Desmodium canadense	20	4
Echinacea pallida	4	4
Liatris aspera	52	12
Monarda fistulosa	8	4
Petalostemum purpureum	4	4
Potentilla arguta	56	12
Ratibida pinnata	68	16
Rudbeckia hirta	24	4
Rudbeckia subtomentosa	4	4
Zizia aurea	3	4
Totals	299	84

TABLE 4. Prairie forbs located in control plots.

SPECIES	TOTAL NO. OF PLANTS	NO. OF PLANTS IN FLOWER
Baptisia leucantha	1	0
Eryngium yuccifolium	2	1
Ratibida pinnata	2	0
Silphium integrifolium	2	0
Silphium laciniatum	4	0
Totals	11	1

In 1981, ½ of the experimental plots were combined for seed before they could be sampled. This northern half was severely matted down and therefore difficult to sample. As the 1981 data are incomplete, they will not be considered further.

Many difficulties arose concerning the identification of forb seedlings during the summer 1982 data collection. For example, *Ratibida pinnata* and *Plantago major* seedlings were difficult to differentiate in the early stages of development. Similarly, distinguishing between *Potentialla arguta* and *Potentilla norvegica* was difficult until *Potentilla arguta* had developed its fourth and fifth leaves. For purposes of this project all *Potentillas* with 3 leaves were assumed to be *Potentilla norvegica.* It was also hard to separate the 3 *Silphium* species with certainty.

PRELIMINARY RESULTS AND DISCUSSION

The control plots were low in prairie forbs, with 11 plants including 5 different species (Table 4). Four of these probably developed from the original seeding, whereas the fifth, *Baptisia leucantha,* was accidentally planted there. The fact that some forbs occurred in the control plots is important in interpreting the experimental results.

The burn-only/seed treatment produced 20 individual plants, an 82% increase over the control plots, but only 3 species were found, all of which appeared in the control plots (Table 5). No plants were in flower as of 6 July 1982. The 20 individuals found represent a maximum germination rate of 1.25%. It is possible that the rate was actually lower, however, because some individuals may not have come from the experimental seeding.

The burn-only/seedling treatment produced 17 individuals, a 54% increase over the control. Of the 7 species present, 3 (*Echinacea pallida, Desmodium canadense,* and *Rudbeckia hirta*) were not present in the control plots, and 3 (*Eryngium yuccifolium, Silphium integrifolium,* and *Silphium laciniatum*) were not planted as seedlings. The survival rate for seedlings planted was 2.9%. Only *Rudbeckia hirta* bloomed (Table 6).

The mow/seed treatment had 15 individuals, a 36% increase over the control. Five species were present, 2 of which (*Echinacea pallida* and *Rudbeckia hirta*) did not appear in the control plots. The results represent a maximum germination rate of 0.94% (Table 5).

The mow/seedling treatment produced the second highest number of individuals and the highest number of species. There were 48 individuals counted, a 336% increase over the control. Twelve species were represented, 8 of which were not present in the control plots and 4 of which were not planted. The survival rate of the seedlings was 16.05% (Table 6).

The ground scarification/seed treatment resulted in 25 individuals, the highest number for the seed experiments and a 127% increase over the control. Six species were represented including 2 (*Potentilla arguta* and *Rudbeckia hirta*) not found in the control. This is the only seed treatment in which *Potentilla arguta* was found. These results represent a maximum germination rate of 1.56% (Table 5).

The ground scarification/seedling treatment produced 67 individuals, the highest of any experiments. There were 11 species found, including 8 not found in the control plots and 3 (*Silphium* spp.) that were not planted. The survival rate for the seedlings was 22.41% with a 2.68% flowering rate (Table 6).

The sod removal/seed treatment contained 10 individuals and 3 species, 1 of which (*Rudbeckia subtomentosa*) was not also found in the control plots. The maximum germination rate was 2.5% (Table 5).

The sod removal/seedling treatment contained 8 individuals and 6 species, 1 of which (*Silphium laciniatum*) was not planted and 4 of which were not found in the control (*Monarda, Potentilla, Rudbeckia,* and *Zizia*). These results represent a survival rate of 9.52% (Table 6).

Caution should be used in interpreting the results of the sod removal treatment as they represent an area only ¼ that of the other treatments. Multiplying these results by 4 for comparative purposes increases the number of individuals found in the seeded plots to 40 and in the seedling

TABLE 5. Percent germination of seeds in plots subjected to various treatment methods.

	BURN ONLY		MOW		GROUND SCARIFY		SOD REMOVAL	
SPECIES	NO.	%	NO. PLANTED	% GERM.	NO. PLANTED	% GERM.	NO. PLANTED	% GERM.
Echinacea pallida			4	50.0				
Eryngium yuccifolium					88	3.4 *		
Potentilla arguta					56	1.8		
Ratibida pinnata	200	4.5 *	200	1.5 *	200	4.5 *	50	14.0*
Rudbeckia hirta			100	1.0 *	100	2.0 *		
Rudbeckia subtomentosa					1	100.0		
Silphium integrifolium	64	9.4 *	64	3.1 *	64	6.3		
Silphium laciniatum	32	15.6 *	32	21.9 *	32	18.8 *	8	25.0*
Totals	1600	1.25%	1600	0.94%	1600	1.56%	400	2.5%

* Rates may be lower than indicated as some individuals may have been present prior to the addition of seed.

TABLE 6. Percent survival of seedlings in plots subjected to various treatment methods.

	Burn only		Mow		Ground scarify		Sod removal	
Species	No. planted	% survival	No. planted	% survival	No. planted	% survival	No. planted	% survival
Coreopsis palmata			40	2.5	40	2.5 *		
Desmodium canadense	20	5.0	20	5.0	20	35.0		
Echinacea pallida	4	25.0						
Eryngium yuccifolium	0	(1)	0	(1)				
Monarda fistulosa			8	37.5	8	50.0	4	75.0
Potentilla arguta			56	5.4	56	16.1	12	8.3
Ratibida pinnata	68	7.4	68	23.5 *	68	38.2 *	16	6.3 *
Rudbeckia hirta	24	8.3 **	24	8.3 **	24	29.2***		
Rudbeckia subtomentosa			4	25.0	4	50.0	4	25.0
Silphium integrifolium	0	(5)	0	(10)	0	(3)		
Silphium laciniatum	0	(2)	0	(4)	0	(2)	0	(1)
Silphium terrebinthinaceum			0	(3)	0	(1)		
Zizia aurea			12	25.0	12	41.7	4	25.0
Totals	299	5.69%	299	16.05%	299	22.41%	84	9.52%

* Rate may be lower than indicated as some individuals may have been present prior to the addition of the seedlings.
** 1 individual flowered
*** 7 individuals flowered
( ) Number of plants found in species for which no seedlings were planted

plots to 32 (germination and survival rates remain unchanged).

Overall, 13 species were found in the experimental plots, with 9 of these not found in the control. All treatments apparently resulted in an increase in the number of forb species over the control. Most also showed an increase in the number of individuals of those species which also occurred on the control plots. In some instances these differences were pronounced—for example, *Ratibida pinnata* in the mow/seedling (Table 6) and the scarification/seedling (Table 6) treatments.

It is interesting to speculate on the causes of the occurrence of non-planted forbs in the seedling treatment plots. These are species which also occur in the control plots and presumably represent pre-treatment conditions. In the mow/seedlings treatment there was a pronounced increase in the number of individuals of *Silphium integrifolium* relative to the control. It is possible that the ground treatment may have caused residual seed to germinate.

Although observations in later years may alter some conclusions, results to date indicate that *Rudbeckia hirta* and *Ratibida pinnata* were the most readily established species regardless of technique. They showed an increase over control for at least 5 of the 8 treatments. Both seem to have established more successfully when introduced as seedlings rather than seeds, a trend that is generally true for all species. Two species—*Coreopsis palmata* and *Zizia aurea*—were found only in the seedling plots. No species were noted only in the seed plots. The scarification treatment was most successful in producing high survival rates for both seed and seedlings. The mow and sod removal treatments were also successful.

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Part 5. Uses of Prairie and Prairie Plants

PRAIRIE INTERPRETATION AT THE MORTON ARBORETUM

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Abstract. The Morton Arboretum offers a variety of prairie interpretation activities. These are designed to increase understanding of what prairie is, its history and importance today, and to enrich one's enjoyment of the prairie. These offerings are of 2 basic types: those for the general public and those for organized groups of school children and others. This paper gives a brief history and description of the Morton Arboretum's Prairie Restoration Project and discusses specific interpretive activities offered.

INTRODUCTION

The Morton Arboretum, 1 of the major botanical institutions in the United States, is an outdoor museum of woody plants located at Lisle, Illinois, 25 miles west of Chicago. It was founded in 1922 as an educational foundation, privately endowed by the founder, Joy Morton. Its present 1500 acres include large tracts of native woodland, wetlands, and meadows, with cultivated woody plant collections interspersed. These collections are arranged in geographical, taxonomic, landscape, and habitat groupings. At the far west end of the grounds is a 15-acre prairie restoration project, begun in 1962.

BACKGROUND OF THE PRAIRIE RESTORATION PROJECT

Although the Arboretum is primarily concerned with trees, shrubs, and woody vines, Joy Morton was aware of prairies and mentioned grasses in his original statement of purpose for the Arboretum. Many of the Arboretum's studies and class offerings have had a strong ecological emphasis, and it is not surprising that prairie, once the dominant original ecosystem of the region, should be of interest to the Arboretum staff. It was first mentioned in 1923 when Henry Teuscher, then Botanist, noted in an inventory that there were remnants of both wet and dry prairie at the east end of the grounds. Later, when May Theilgaard Watts was Naturalist at the Arboretum from 1942 to 1961, these remnant prairies became field trip sites for many Arboretum classes. Mrs. Watts became very interested in prairie and wrote about it in her book, *Reading the Landscape*. She also led the effort in the sixties to establish the Illinois Prairie Path along an abandoned railroad right-of-way west of Chicago.

Studies of the prairie flora intensified after 1960 when Floyd Swink joined the Arboretum staff. Floyd was a field botanist who had been studying Chicagoland plants since the 1940s and had become highly knowledgeable about the locations of remnant prairies throughout the region and their specific plants. Beginning in the summer of 1961, other botanists accompanied Floyd in his collecting, including Ray Schulenberg, then Assistant Propagator at the Arboretum; Dr. Robert Betz of Northeastern Illinois University, who is now noted for his work with preserving remnants of original prairie and the pollination of milkweeds; David Kropp, a landscape architect who has worked extensively with native plants; and many others.

Thus there was already a vital interest in prairie in 1962 when the Arboretum acquired a sizable acreage of open farmland on its west border. It was decided that the best use of the land would be for re-creating a prairie similar to the one at the University of Wisconsin Arboretum. To accomplish this, Clarence Godshalk, then Director of the Arboretum, appointed Ray Schulenberg as Curator of Native Plants, and gave him the responsibility of developing such a prairie restoration. Ray set about this project with energy and diligence and by 1968 had established 15 acres of prairie, using a variety of methods. Summer employees and volunteers assisted in gathering seed, planting, transplanting and weeding the prairie during these years. In 1968 Ray was made Curator of the Herbarium but continued to oversee the prairie with the assistance of summer helpers.

Even as the Arboretum was developing a restored prairie on its west side, the remnant original prairie at the east end of the Arboretum was destroyed, unfortunately, when a Northern Illinois Gas Company easement went through that area in 1974.

Ray Schulenberg remained in charge of the prairie until 1979 when he became Curator of Plant Collections. In 1980 the responsibility for the prairie was transferred to Patricia Armstrong, the Assistant in Education. I had been on the Arboretum staff for 10 years and had studied the prairie under May Watts and Ray Schulenberg. I began to recruit and train some 60 prairie volunteers to help with the work of collecting seed, removing weedy invaders, and other tasks associated with maintaining the prairie. I also developed several study units about the prairie, and began to use the prairie as a theme for poetry-writing classes at the Arboretum and related artistic activities.

THE PRAIRIE RESTORATION PROJECT

The Morton Arboretum Prairie Restoration is located on the western boundary of the Arboretum, accessible to visitors who park in a lot about a half mile away. The prairie is intersected by Willoway Creek, with a 3½-acre section located north of the creek, a 12-acre section on a hillside farther south, and about 4 acres of old field and roadway in between the two. The eastern edge of the prairie merges into shrubby fields and Arboretum woodlands. Present in the south section is a large bur-oak (*Quercus macrocarpa*), which is gradually becoming surrounded by younger trees.

Around the perimeter of the prairie are wide, mowed fire breaks. These are also used as places where large groups of visitors may walk or sit to study the prairie. Within the prairie the paths are very narrow, leading walkers single-file in a clockwise direction along three loops. Visitor regulations include staying on the path, moving one way only, not picking plants, and not smoking in the prairie.

PRAIRIE INTERPRETATION ACTIVITIES AT MORTON ARBORETUM

Goals and General Content

The Morton Arboretum offers a number of different kinds of interpretive activities designed to meet the needs of adults and children of all ages. For the general public there are nature rambles, a self-guided nature trail with a printed guide, and a variety of classes, field trips and special events listed in the quarterly *Program of Educational Acitivites.* For organized groups, a series of different field trip experiences is offered, varying in length of time, and depth of study.

By encouraging people to use their senses in observing and enjoying the prairie, we try to develop a sense of wonder and appreciation for the beauty and complexity of our natural world, how its parts interact, and the role of individual species in the functioning of the entire system. We help each group understand some of the laws and cycles which occur in nature and the effects of human interference upon them by appealing to their intellectual and emotional capacities. We hope that this experience will help nurture an attitude of caring about our planet Earth, a desire to protect prairie and other ecological areas, and a commitment toward living in harmony with nature, both now and in the future.

On every prairie trip we try to answer the following questions, but the depth to which we cover the questions depends upon the age of the group and the length of time we have with them.

(1) What is (was) prairie?
(2) What kinds of plants and animals are (were) adapted to the prairies?
(3) How do prairies differ from old fields and lawns?
(4) How did (do) the Indian, pioneer, modern people, we (you) feel about the prairie?
(5) What happened to all the prairie that was once here?
(6) How does species diversity in a lawn or old field compare to that of a prairie?
(7) How does the energy required for maintenance of a lawn compare to that of a prairie?
(8) What is the place of fire in prairie ecology and succession?
(9) Should we preserve or restore prairies today? Why or why not?
(10) How do we preserve and restore a prairie?
(11) How should we treat a prairie remnant or restored prairie?
(12) What is the relationship between prairie and soil and the food production of Illinois farms for the world?
(13) What is happening to our Illinois farms?
(14) What can we do about it?
(15) What are some ways we can experience the prairie aesthetically?

In order to answer the preceding questions, we try to include most or all of the following activities on each guided trip.

(1) Reading historical descriptions and quotations about the prairie.
(2) Reading and/or writing poetry about the prairie.
(3) Seeing, hearing, feeling, smelling, and tasting the prairie.
(4) Looking for, stalking, catching, and studying insects of the field and/or prairie.
(5) Sitting alone to draw, write, and/or feel the prairie.
(6) Talking about the way different people used the prairie (reading stories and poetry).
(7) Talking about pioneers, modern farms, food production, fertilizer, herbicides, pesticides, soil erosion, and urban development.
(8) Examining and comparing the plants and animals in various plots.
(9) Discussing values and ethics that relate to prairie restoration and preservation.

Interpretive Programs for the Individual Visitor

Anyone who comes to the Morton Arboretum may walk out to our Prairie Restoration Project and wander the trails at his or her leisure. Because the prairie is an ecosystem easily disturbed and degraded, it is perhaps fortunate that our prairie is located some distance from the parts of the Arboretum most heavily used by visitors. Thus, those who go to the prairie are usually those who really want to see it and will make the extra effort to get there.

To help the individual visitor learn more about prairie, we have one clearly marked trail with numbered posts. A prairie trail leaflet, available from the Visitor Center gives information about each numbered stop and about some specific plants and prairie in general.

Interpretive Programs for Organized Groups

Most of the prairie interpretation activities at the Morton Arboretum are designed for school groups accompanied by their classroom teachers. These groups generally visit between September and November. (Since our restored prairie has little spring flora and is burned every spring as a means of weed control, there is not much to see there until June. By then school is closing for the summer.) In the fall we offer 4 different types of prairie activities for school children. A fee is charged for those led by our naturalist-guides. Information on fees and scheduling is available by calling or writing the Registrar, Morton Arboretum, Lisle, Illinois 60532; telephone 312/969-5682.

Teachers' and Leaders' Workshops. For groups who do not wish to pay for a naturalist-guide or who prefer to lead their own groups, we offer a teachers' workshop so that they and their assistants can learn how to conduct a field trip in our prairie.

During the course of the workshop, the teacher or leader will learn where the Prairie Trail is, how to get around in the Arboretum, and what kind of activities are possible on the Prairie Trail. Each participant receives an 18-page booklet with directions, maps, suggested activities, lists of plants and animals, drawings, and a resource bibliography.

General Prairie Trip for Schools. The usual school prairie trip is a 1½- to 2½-hour experience led by a naturalist-guide.

The main ideas for the school field trip are these: One hundred-fifty years ago, much of Illinois was covered by tall grasses and prairie wildflowers. Settlers destroyed most of the prairie by reducing wildfires and plowing the land. Today the few patches of original prairie that remain are supplemented by restorations such as the one at Morton Arboretum.

Supporting and supplementary concepts introduced in the school field trips are as follows:

> Tallgrass prairie is a plant community characterized by many species of beautiful plants; an old field contains few species, most of them weeds.
>
> On most sites in our area (given no interference) climax vegetation of hardwood forest would be produced by our climate and soils. Fires once kept the trees from advancing on the grasslands; in more recent times, man with his axe and bulldozer has reduced the areas of forest.
>
> Prairies have many values for humans; we will benefit by preserving good examples.
>
> Prairie plants and animals are adapted to open, sunny, often hot and dry locations.
>
> Deep-rooted prairie plants produce a deep, rich topsoil which is the best farm soil in the world.
>
> The bur-oak is a pioneer woody plant that occurred at the edge of the prairie or in wooded islands within it called "openings."
>
> Prairie restoration involves establishment of a large variety of prairie plants (either by direct sowing of seed or transplanting), followed by weed control—first by hand, later through the use of controlled burning.

The total experience is conducted outdoors in the prairie, appealing to the senses of the student. Pencils and papers may be used to draw or write poetry, but generally no worksheets or notes are taken. Basic activities include discussing and reading, touching and experiencing, drawing and writing, listening and observing.

Advanced Prairie Trip for Schools. For groups who want something more, we have a 4-hour field trip called "Our Illinois Prairie Heritage." An hour and a half is spent in the prairie, largely doing the same activities as are done on the regular prairie trip. The group then spends another half hour studying the plants and animals in an old field and comparing them to what they observed in the prairie.

During and after a lunch period in the Thornhill Conference Center, the naturalist-guide in charge leads the students to explore prairie displays and to form their own answers to a set of supplementary questions. There are several displays, each designed to help the students find the answers to the summarizing questions.

(1) Map of presettlement vegetation of the state of Illinois.
(2) Drawing of prairie plants showing their deep root systems.
(3) Surviving natural prairies of the Chicago region shown on an urban map.
(4) Newspaper clipping about the John Deere prairie plow.
(5) Map of Illinois showing farm income and production.
(6) Soil erosion facts.
(7) Boxes of sand, subsoil, forest soil, prairie soil, and blacktop highway.
(8) Boxes of corn and soybeans with cobs and pods.
(9) Boxes of food items made from corn and soybeans.

The naturalist-guide then helps the group summarize their whole prairie heritage experience by discussing their answers to these questions:

(1) How is the land that once was prairie land used today?
(2) How important are Illinois farms to people throughout the world?
(3) What was the role of prairie plants in developing Illinois soil?
(4) What has happened to the prairie?
(5) What is happening to the soil?
(6) What can we do to preserve our Illinois prairie heritage?

Resident Program. Prairie study is one of the units included in our 2½-day resident program for fifth graders. We run this program for about 12 weeks, 6 in the spring and 6 in the fall. All of the teaching is done by Arboretum naturalist-guides. The program includes a study of the Arboretum woodlands, wetlands, meadows, and plant collections as well as the prairie.

In the spring, ponds are emphasized, as the prairie is less developed. In the fall when the ponds are dry, the prairie is lush and is emphasized, along with meadow and lawn comparisons, making a 4- to 5-hour study.

Learning objectives for this study are:

(1) To discover the beauty and diversity of a prairie as compared to that of a lawn or old field.
(2) To experience the feeling of prairie and express it by drawing and writing impressions while there.
(3) To observe adaptations in prairie plants.
(4) To think about our lost prairie heritage and what we can do to preserve it.
(5) To learn the important role of insects in prairie ecology and study plant/insect interrelationships.

Activities include the following:

(1) Comparing the plants and animals present in a well-tended lawn, an old field, and the prairie, and filling out data sheets about each plot.
(2) Creative drawing and writing in the prairie.
(3) Checking animal track stations.
(4) Catching and studying an insect.
(5) Campfire songs and stories about Indians and pioneers.
(6) Making reports on prairie plants and animals.

The summarizing activities include making a mural on prairie life and discussing how the prairie benefits us—economically, aesthetically, and ecologically. The following questions are discussed:

(1) Why is Illinois called the Prairie State?
(2) What is the relationship between Illinois agriculture and prairie history?
(3) What is unique about prairie?
(4) What animals have become extinct or endangered by the destruction of the prairie?
(5) How did the Indian use the land as compared to how the white man used it?

Other Arboretum Sponsored Activities Relating to Prairie

Arboretum Classes. Throughout the year, but mostly in summer and fall, the Morton Arboretum offers many classes and special events centered around prairie. There are creative writing classes which include reading as well as writing about prairie. There are wildflower and weed identification classes for learning about the plants of prairies and fields. There are field trips to visit our prairie and other local prairies to see the plants and learn about the prairie environment. At times we offer "prairie pedaling" when people can bike out to the prairie and then take a walk. And there are seasonal natural history classes (for adults and children) where at least 1 session is spent studying the plants and animals of the prairie.

Nature Rambles. On Saturdays or Sundays throughout the year, the Arboretum offers free nature rambles led by naturalist-guides. These informal walks are designed for the general public and feature prairie several times in the summer and fall.

Prairie Day. For the past 2 years we have held a Prairie Day on a Saturday in July for children (accompanied by their parents) to become better acquainted with prairie. Naturalist-guides dress up in old-fashioned costume and help students make sun bonnets and hats before they all ride out to the prairie in a horse or tractor drawn hay-rack. A small fee is charged to cover the cost of a prairie picnic (old-fashioned cookies and beverage) served on gingham tablecloths in the prairie. Sense-oriented displays of plants, animals, and pioneer life complete the half-day experience.

Volunteer Training. In addition to all of the above, the Morton Arboretum has a corps of active Prairie Volunteers who spend many hours a year working in the prairie collecting and planting seeds, pulling weeds and cutting brush, maintaining the trails, and burning the prairie. This is probably one of the best ways to learn about and become intensely involved in prairie while having a good time with other people of similar interest. There are several enjoyable social events for prairie volunteers as well as training and work sessions.

CONCLUSION

There are probably as many ways to interpret prairie as there are interpreters. These are just some of the ways we have found useful at the Morton Arboretum. Further information about any of the activities or other interpretive programs, may be obtained by writing or calling the author (312/968-0074).

THE COMMERCIAL PRODUCTION OF PRAIRIE PLANTS

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Abstract. A questionnaire was mailed out in August 1981 to commercial producers of prairie plants to ascertain (1) the relative importance of local prairie remnants as plants and seed sources, (2) the role of mechanization in harvesting prairie seed, and (3) the markets available to producers of prairie plants. The results of this survey are presented in a table and discussed in text. In general, seeds are the most common means of producing prairie plants commercially, local prairie remants are very important sources for these seeds, most seed is sold to customers within the producer's own state, and government agencies are one of the most important buyers.

INTRODUCTION

The purpose of the survey was to ascertain the status of commercial prairie plant and seed production, with particular interest in 3 areas: (1) the relative importance of local prairie remnants as plant and seed sources, (2) the role of mechanization in harvesting prairie seed, and (3) the markets available to producers of prairie plants.

A survey questionnaire was designed and mailed in August 1981 to 44 commercial producers of prairie plants, as well as to a few nurseries that deal mostly in wildflowers. The latter were included on the chance that they might also be propagating prairie species. Forty-eight percent of the questionnaires were returned, and the map (Fig. 1) shows the approximate geographical locations of the 21 respondents.

SOURCES

The first part of the survey was designed to determine the relative importance of the 3 major sources of prairie grass and forb seed—local prairie remnants, propagation blocks, and purchases from other producers.

It was found that 63% of the companies use local prairie remnants as seed sources, 21% obtain over half of their grass seed from local remnants, and 16% obtain more than 80% from this source (Table 1). Nursery-operated propagation blocks are less important, with 58% of the producers obtaining some seed from propagation blocks, 16% obtaining over half and 11% obtaining more than 80% of their grass seed from propagation blocks. The purchase of prairie grass seed is the most important source, with 79% of the companies purchasing some grass seed, 42% purchasing more than half their grass seed, and 26% purchasing more than 80%. It should be noted that purchases are sometimes made from people who harvest local prairie remnants, as well as from contract growers, and therefore local remnants may be an even more important source of prairie seed than the survey results indicate.

A somewhat similar pattern is found in the sources of prairie forb seed. Seventy percent of the respondents use local prairie remnants as a source for forbs, 40% of them for over half and 17% for more than 80% of their forb seed. Fifty-nine percent of the producers obtain forb seed from their own production blocks, 18% obtain more than half, and 6% more than 80% from this source. Again, purchase is the major source, with 76% of the companies purchasing some forb seed, 42% purchasing more than half, and 30% purchasing more than 80%.

HARVESTING

The second purpose of the survey was to study the role of mechanization in harvesting prairie grass seed. While collecting by hand is widely used and 85% of the respondents use some hand labor, most companies also use machinery, 77% using unmodified harvesters and 45% using modified ones. Thirty-eight percent of the producers use hand labor for harvesting over half of their prairie grass seed, 38% use unmodified machines to harvest over half of

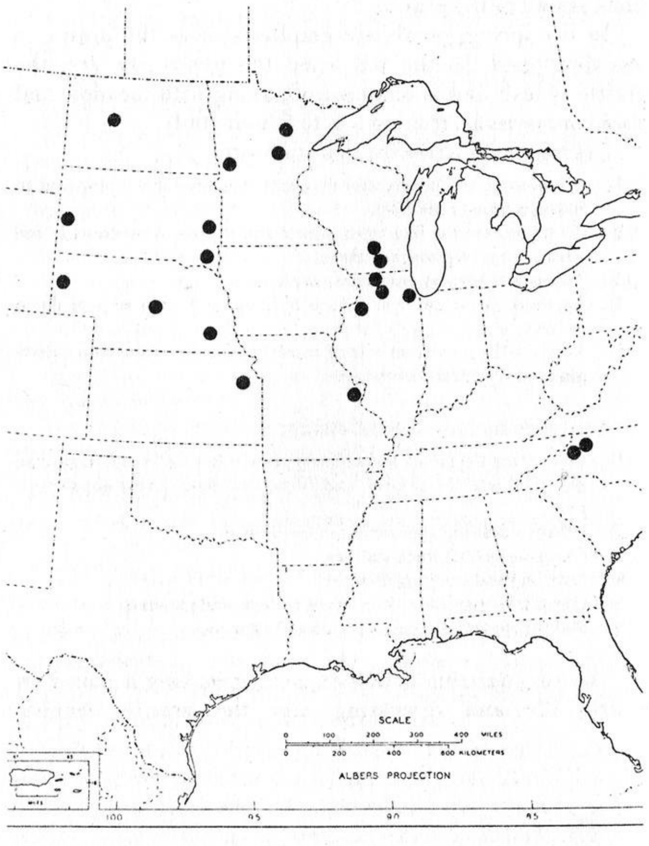

FIG. 1. Map showing approximate locations of respondents to questionnaire.

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TABLE 1. Information compiled from questionnaire. The first number in a column refers to the number of respondents in that category; the corresponding percentage is in parentheses. The Total column gives the number of respondents answering that question. For example, in the first entry, 7 of 19 respondents (37%) indicated that they did not utilize local prairie remnants as a source for their grass seed and 3 respondents (16%) obtained from 1% to 20% of their grass seed from local prairie remnants.

	NONE	1-20%	20-40%*	60-80%	80-100%	TOTAL
What Percentage of Your Grass Seed Originates from						
Local remnants	7 (37%)	3 (16%)	5 (26%)	1 (5%)	3 (16%)	19
Own production	8 (42%)	5 (26%)	3 (16%)	1 (5%)	2 (11%)	19
Purchase	4 (21%)	5 (26%)	2 (11%)	3 (16%)	5 (26%)	19
What Percentage of Your Forb Seed Originates from						
Local remnants	5 (30%)	5 (30%)	0 (0%)	4 (23%)	3 (17%)	17
Own production	7 (41%)	3 (17%)	4 (23%)	2 (12%)	1 (6%)	17
Purchase	4 (23%)	6 (36%)	0 (0%)	2 (12%)	5 (30%)	17
What Percentage of Your Native Grasses Is Harvested by						
Hand labor	2 (15%)	5 (39%)	1 (8%)	2 (15%)	3 (23%)	13
Unmodified machine	3 (23%)	3 (23%)	2 (15%)	3 (23%)	2 (15%)	13
Modified machine	7 (55%)	2 (15%)	2 (15%)	0 (0%)	2 (15%)	13
What Percentage of Your Sales Is of						
Seeds	1 (5%)	1 (5%)	3 (15%)	2 (10%)	13 (65%)	20
Seedlings	12 (60%)	2 (10%)	2 (10%)	1 (5%)	3 (15%)	20
Asexual propagules	16 (80%)	2 (10%)	2 (10%)	0 (0%)	0 (0%)	20
What Percentage of Your Sales Is Made						
Locally	7 (37%)	10 (52%)	2 (11%)	0 (0%)	0 (0%)	19
In-state	0 (0%)	1 (5%)	6 (32%)	7 (37%)	5 (26%)	19
Out-of-state	4 (21%)	5 (26%)	7 (37%)	2 (11%)	1 (5%)	19
What Percentage of Your Sales Is Made to						
Individuals	4 (21%)	10 (52%)	2 (11%)	2 (11%)	1 (5%)	19
Contractors	4 (21%)	7 (37%)	7 (37%)	0 (0%)	1 (5%)	19
Corporations	8 (42%)	4 (21%)	2 (11%)	5 (26%)	0 (0%)	19
Government agencies	4 (21%)	2 (11%)	10 (52%)	1 (5%)	2 (11%)	19
Other	12 (63%)	1 (5%)	3 (15%)	1 (5%)	2 (11%)	19
What Percentage of the Seed You Produce is						
Used in own work	5 (30%)	6 (36%)	2 (12%)	1 (6%)	3 (17%)	17
Sold	1 (6%)	2 (12%)	1 (6%)	2 (12%)	11 (64%)	17

*The category of 40-60% was inadvertently left off the questionnaire.

their seed, and 15% harvest that amount with modified machines. The survey showed that producers in states west of the Mississippi River use machinery much more extensively than producers in states east of that river.

There are 3 methods used for propagating prairie plants for sale—seeds, seedlings, and vegetative propagules. Seeds are most commonly used, with 95% of the companies offering seeds. Seeds account for over half of the production for 75% of the companies and over 80% for 65% of the companies. Seedlings are used by 40% of the companies, and vegetative propagules by 20%, but it is clear that seedlings and vegetative propagules play a minor role.

SALES

Seed of prairie species is produced commercially for 2 principal reasons: to sell to others and to use in a company's own contract work. Ninety-four percent of the companies produce seed for sale and 70% for their seed in their own contract work. Sixty-four percent of the respondents sell more than 80% of their seed, while only 15% use more than 80% of the seed they produce in contract work.

The third part of the survey examined the markets available to producers. Sales of prairie seeds are made to a fairly diverse group of consumers, such as private individuals, contractors, corporations, and government agencies. Sales are rather evenly divided among these consumers, and 16% of the respondents indicated that they made more than half of their sales to individuals, 5% sold more than half to contractors, 26% of the companies sold over half to corporations, another 16% made half of their sales to government agencies, and 16% reported half of their sales to various other consumers. It appears that government agencies are the largest consumer of prairie seed; they buy more than half of the seed produced by 16% of the respondents and over 80% of production of 11% of the respondents.

Prairie plant producers sell their seed locally, in-state, and out-of-state. All of the producers responding to the survey sell to in-state customers, 63% of them sell locally, and 79% have out-of-state customers. Local sales are relatively minor and none of the respondents sells over half of their seeds within a 10-mile radius. In-state sales constitute the largest market, with 63% of the producers selling over half and 26% selling over 80% of their production within their own state. The out-of-state market is also rather small, with only 16% of companies having more than half of their sales to out-of-state customers.

Seed certification is allied to production and harvesting. Only 29% of the companies certify all or part of their seed, and only 14% of them guarantee seed viability. Certification and guarantees are difficult problems for seedsmen because of the sheer number of prairie species, complex dormancy mechanisms, the logistics of sampling each lot, and the fact that many states have no experience in testing prairie species.

FUTURE

The survey indicates that producers of prairie seed are optimistic about the future of their industry, with 75% of them anticipating some degree of growth in the coming years. The preservation of native prairie remnants and their gene pools is crucial both for the conservation of this once widespread ecosystem and also for use as seed sources for the prairie plant production industry. However, commercial enterprises must be careful not to destroy prairie remnants through unscrupulous collecting. As the industry continues to expand, producers will, it is hoped, grow more of their own seed in production blocks. Another important consideration, which was not addressed in this survey, is that many seedsmen utilize cultivars of both grasses and forbs developed in plant material centers. The volume of seed produced from cultivars is probably very high, and the use of such seed greatly reduces the diversity of gene pools.

TRANSPORTATION AND NATIVE VEGETATION: OLD ASSOCIATES REJOIN TO SOLVE MODERN PROBLEMS

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Abstract. From the time Conestoga wagons first crossed the Midwest, native grasses and forbs have been close associates of man's transportation corridors. This paper outlines the move away from the natives as cover on highway rights-of-way and toward maintenance-intensive cool-season species in the 1950s, the resultant problems created by reduction in maintenance funding in the 1970s, and the return to natives as problem-solvers of the 1980s. A specific project in the Chicago Metropolitan Area is examined which illustrates current practices and demonstrates cost-effectiveness through utilization of native vegetation to solve practical problems.

It was there all the time, and I suppose someone should have recognized it earlier for what it could be. It had been on the job, quite by accident, since before the Industrial Revolution pushed its steel ribbons through the Mid-American grassland in the 1850s. The recent history of the great native grasslands of this country and that of surface transportation have been firmly, if not concisely, interwoven.

It was only when man began to believe that he understood how to perform nature's work better than she did on her own, that transportation, especially highway transportation, separated from its previously symbiotic relationship with the native landscape.

In the early 1950s America began constructing what was to be a nation-wide network of superhighways, later to be designated the Interstate Highway System. In planning this system, the manicured roadsides of Europe, the Autobahn of Germany, and the East Coast Parkway System became the maintenance role models, however inappropriate, for the Midwest highways. Thus a system was developed in a relatively short period of time which relied upon species that required a high maintenance diet. Park-type mowing, high levels of fertility, and intense cultivation was the rule of the day, and most native plants and communities were forgotten, sprayed into extinction, or bypassed as incompatible with that rule.

In 1974 the rules changed with the Arab oil boycott and escalating inflation. All budgets, including that of the transportation agencies, began to mandate economies in operating practices; mowing and roadside maintenance were early, painless cuts that could be made. With the

TABLE 1. Native grass seeding locations.

AREA NUMBER	SIZE (ACRES)	DATE PLANTED	SOIL TYPE
NB-1	1.6	7-14-80	Clay/Stone
NB-2	2.3	7-14-80	Clay/Stone
NB-3	1.6	7-15-80	Sandy Clay/Stone
NB-4	1.3	7-15-80	Sandy Clay
NB-5	1.2	7-29-80	Sand
NB-6	3.7	6-29-81	Silty Clay/Stone
NB-7	2.0	7-1-81	Clay/Stone
SB-1	2.4	5-27-81	Silty Sand
SB-2	2.4	5-27-81	Silty Sand
SB-3	3.0	6-5-81	Silty Sand
SB-4	9.6	6-5-81	Silty Sand
SB-5	1.4	6-17-81	Topsoil over Silty Clay/Stone
SB-6	1.7	6-17-81	Topsoil over Silty Clay/Stone

reduction or cessation of roadside maintenance, problems began to surface. Weeds and woody growth began to invade turf areas, and the turf quality began to decline due to the lack of mowing, fertilizer and water.

Recognizing that practices utilized for the past 20 years were no longer satisfactory was fairly simple; determining what to substitute was not. In addition to enduring and thriving, successful highway plantings must meet a number of other requirements.

The roadside environment, particularly in the urban area has always been hostile to plant life. Soils, usually some type of subsoil, are extremely variable in structure, quality and origin, and usually contain a considerable admixture of rock, broken concrete, and building refuse. Often they are highly compacted, poorly drained, and saturated with road salt and motor oil and fuels. Turf and other plants in a roadside environment are also exposed to salt spray, lead, and a host of other airborne pollutants, drought, insect pests and weed infestation. When the existing environment and reduced maintenance practices are combined, turf quality declines and the condition of roadside vegetation is very sorry indeed.

In order to establish grasses economically upon large areas of the right-of-way, they must be able to be established from seed fairly rapidly and lend themselves to mechanical planting over a large area. Roadside grasses must be able to tolerate a wide variety of conditions even on the same site, and to respond to almost no post-planting care. In addition, the grasses must be highly competitive in

TABLE 2. Grass and forb mixture, Edens Expressway.

SPECIES	SEEDING RATE*
Grasses	96 pounds/acre (17 kg/ha)
Lolium perenne, perennial rye	25
Avena sativa, seed oats	50
Andropogon scoparius, little bluestem	11
Bouteloua curtipendula, side oats grama	6
Elymus canadensis, prairie wild rye	1
Panicum virgatum, prairie switchgrass	2
Sporobolus heterolepis, prairie dropseed	0.5
Stipa spartea, porcupine grass	0.5
Forbs**	2 pounds/acre (0.4 kg/ha)
Amorpha canescens, lead plant & inoculant	
Asclepias tuberosa, butterfly weed	
Aster azureus, skyblue aster	
Aster laevis, smooth aster	
Baptisia leucophaea, cream baptisia & inoculant	
Camassia scilloides, wild hyacinth	
Ceanothus americanus, New Jersey tea	
Cirsium hillii, Hill's prairie thistle	
Coreopsis palmata, prairie coreopsis	
Dodecatheon meadia, shooting star	
Echinacea pallida, pale purple coneflower	
Eryngium yuccifolium rattlesnake master	
Gentiana andrewsii, closed gentian	
Gentiana puberula, prairie gentian	
Heuchera richardsonii, alum root	
Liatris aspera, rough blazing star	
Liatris pycnostachya, prairie blazing star	
Monarda fistulosa, bergamot	
Parthenium integrifolium, prairie quinine	
Pedicularis canadensis, wood betony	
Petalostemum candidum, white prairie-clover & inoculant	
Petalostemum purpureum, purple prairie-clover & inoculant	
Potentilla arguta, tall cinquefoil	
Prenanthes racemosa, rattlesnake root	
Ratibida pinnata, prairie coneflower	
Rudbeckia hirta, black-eyed susan	
Rudbeckia subtomentosa, sweet coneflower	
Solidago rigida, stiff goldenrod	
Veronicastrum virginicum, Culver's root	
Annuals	16 ounces/acre (0.2 kg/ha)
Cichorium intybus, wild chicory	2
Coreopsis lanceolata, lance-leaved coreopsis	4
Gaillardia pulchella, indian blanket	5
Papaver rhoeas, corn poppy	0.5
Ratibida columnaris, upright prairie coneflower	1
Rudbeckia sp. "Triploid"-black-eyed susan	1.5
Silene armeria, sweet William	2

* Seeding rate for grasses is pounds of pure live seeds per acre; for annuals, ounces per acre.

** A mix of not fewer than 20 of 29 listed species was used.

TABLE 3. Maintenance cost comparison (in dollars) of native and non-native turf, acre basis, 1980 season.

WORK ITEM	NON-NATIVE	NATIVE
Initial Seeding		
Seed bed preparation & planting	$ 770	$1850
Emulsified Asphalt/Mulch	1120	1120
Fertilizer	1385	0
Subtotal, Initial Seeding	3275	2970
First-Year Maintenance		
Mowing	70*	70**
Turf Fertilization	400	0
Herbicide	40	0
Subtotal, First Year Maintenance	510	70
Annual Maintenance***		
Year 2	37	0
Year 3	38	0
Year 4	39	39
Year 5	80	0
Subtotal, Maintenance Years 2-5	194	39
GRAND TOTAL ANNUAL MAINTENANCE & ESTABLISHMENT AFTER 5 YEARS	$3979	$3079

* 4 mowings at $17.50.

** 2 mowings at $35.00 (2 × regular mowing due to grass height).

*** Annual Maintenance—Mowing costs escalated $1/Mowing/Year.
"Typical Highway Maintenance" (non-native grass):
2 mowings/year
Herbicide at $40/acre every 4 years
No fertilizer
Native Plant Maintenance:
Mow once every 3 years at 2 × regular mowing cost due to height (in areas where burning is permissible, could use burning costs)

an exposed area, and the mature stand must be aesthetically pleasing.

Although the use of native grasses seems now to be a logical solution to part of the problem of what to plant on the roadsides, it has become so only since the commercial availability of seed in sufficient quantities became a reality.

In the spring of 1979 the Illinois Department of Transportation began reconstruction of Interstate 94, also known as the Edens Expressway. This route was constructed in the 1950s as a parkway-type facility, and is located parallel to Lake Michigan, stretching from Chicago north into the suburbs. The plan was to remove and replace the pavement, and to utilize the right-of-way for all construction functions including stockpiling and processing of material from the recycled pavement. All of this activity would destroy the existing landscape and make restoration quite difficult. Since conditions for this project were representative or more difficult than the normal urban highway site, it was decided to utilize the Edens project as a demonstration of how native grasses and forbs could provide an economical and practical cover for problem sites.

The first sites were seeded in July 1980, with seedings completed in the summer of 1981. A total of 3.2 ha (8 acres) were seeded in 1980 with 12.6 ha (31.3 acres) seeded in 1981 (Table 1). Seeding was done with a Truax Drill at the mixture and rates shown in Table 2. A cover crop of oats, perennial rye and some annual flowers was used to avoid soil erosion and a bare look the first year. The actual composition of forbs in the mix was variable according to seed availability in the local market at the time of planting. After seeding, the area was mulched with straw at a rate of 0.87 metric tons/ha (2 tons/acre).

At the end of the 1981 growing season, growth was quite encouraging and thus far in 1982 results are very good. The economics of native grassland seems to be very good, too, based upon actual bid prices as compared to a "normal" highway treatment (Table 3). It would appear that as long as seed availability is not a problem, native grass seedings can be installed and maintained during the first 5 years on at least a "break-even" basis with conventional "cool-season" seedings, and perhaps with some advantage to them as seed prices stabilize.

The gently swaying grasses interspersed with many hued jewels of flowers act not only as a versatile ground-cover suitable to the extreme conditions adjacent to our highways, but as a pleasant visual reminder of our grassland heritage.

EVALUATING THE SUCCESS OF PRAIRIE RESTORATIONS

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Abstract. Available prairie assessment techniques are based on comparison with natural prairie. However, prairie restorations are usually simplified versions of natural prairie. After assessing 4 prairie plantings in the area of Minneapolis, Minnesota, with the Howell (1981) technique, I developed assessments that judge by comparison with simplistic restoration goals rather than natural prairies. The biological approach examined the sites based on a species list noted on a walk through each site. The technique's advantages include (1) minimal field study, (2) minimal botanical expertise, (3) no need for detailed records required in scientific comparisons, and (4) comparison relative to our goals. The visual assessment analyzed the sites based on their appearance. After examination of the literature, I concluded that 3 visual elements (grasses, flowers, and space) combine to give us the visual essence of prairie. Assessing these elements in terms of unity, memorability, and intactness in this prairie landscape, yielded a 1-page assessment form. This tool is easily used on a site visit by people with minimal botanical knowledge. This approach attempts to deal with a fact that the majority of people who judge a recreation of prairie often do so based only on what they see. After further study, such simple tools could be utilized by landscape architects, biologists, nurserymen, and others with varied backgrounds in a consistent and reliable manner necessary for decision making.

INTRODUCTION

Environmentally sound solutions make economic sense for a growing number of landscape problems. Restoration of prairie, woodland, and wetland ecosystems to urban and suburban sites is 1 of these solutions. It is the responsibility of the landscape architect, along with biologists, engineers, nurserymen, and others involved in restoration efforts, to implement that solution as successfully as possible. Noticeable success will support environmental approaches, even if economic pressures ease.

To judge success in prairie restorations, I developed assessments that could improve the design and management of future restorations. I tried to devise "simple"

TABLE 1. Natural Areas Quality (Howell 1981) assessment applied to case studies.

TEST STATISTICS	SITES (AND DATES OF ESTABLISHMENT)* SH (1978)	PI (1976)	DD (1973)	BD (1972)
Number of natural species	60	60	60	60
Number of prevalent species	75	75	75	75
% exotic species	30	30	30	30
% quadrats with exotics	25	75	25	25
	190	240	190	190

* SH is Spring Hill; PI, Pike Island; DD, Doug Dayton residence; and BD, Bruce Dayton residence.

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techniques which persons of varied backgrounds could use and still produce consistent results necessary for decision making.

DEVELOPMENT OF THE TECHNIQUES

Four existing projects were chosen from the files of Prairie Restorations, Inc. of Princeton, Minnesota, a firm that has been installing prairie plantings for more than 10 years. All sites were located near Minneapolis: Spring Hill Conference Center, Pike Island Nature Center, Doug Dayton residence, and Bruce Dayton residence. They were selected on the basis of similarities in size, location, environmental conditions, land-use history, seed mix and rates, planting procedure, and subsequent management.

These case studies were contracted installations, not closely controlled scientific experiments. The goal in their construction was to re-create the semblance of prairie rather than the complex natural prairie that once existed in the region. "Seed plantings will almost always be simplifications in that there will initially be fewer species than in a natural prairie" (Morrison 1980).

BIOLOGICAL ASSESSMENT

In order to assess the 4 sites in terms of species composition a number of years after planting, field sampling was done with a stratified random sampling method using transects. The existing vegetation was then assessed by the quality analysis technique of Howell (1981). Its aim is to assess natural grasslands for their potential for ecosystem research, education, recreation, and hunting. When applied to the case studies, this analysis indicated that Pike Island was the most successful restoration in terms of diversity and naturalness (Table 1).

This site earned a quality rating of 240, medium quality compared to natural stands, while the other 3 received low quality ratings. Pike Island excelled because only 43% of the quadrats showed exotics. It appeared that a low diversity of species, mainly grasses, quickly took over the site, outcompeting the exotics. For my application, the Howell rating weighted "% Quadrats with exotics" too highly.

In my estimation, Pike Island had the least desirable composition and lowest visual quality. Consequently, I devised an assessment of the composition and visual quality (to be explained later), relative to our more simplistic goals. The rationale was that intentionally planted, long-lived species and species native to prairie are desirable; whereas species that are volunteers, short-lived, or exotic to prairie are undesirable.

These species characteristics were applied to individual species based on descriptions of Curtis (1959), Heitlinger (1979), P. Jensen (pers. comm.), Swink (1969), and Zimmerman (1959). The results of a species list compiled from a walk through each site were combined with a matrix of these characteristics. Positive and negative values were assigned and totaled. Each value is divided by the total species to decide positive to negative ratio. Thus, a relative comparison of success can be made between sites. Further case studies are necessary to develop a wide basis of comparison and general interpretations of success.

When the technique was applied to the 4 case studies, the most successful planting was found to be the oldest 1 (Table 2). The Bruce Dayton site contained the largest number of species intentionally planted; the highest amount of long-lived species, and the most plants native to prairie. The existing amounts of exotics and short-lived plants appeared to result from the proximity of woodland propagules and gopher mound activity. However, the youngest site, Spring Hill, placed second. Improvement appeared possible by reducing the exotic species by burning. Pike Island's low diversity suggested a need for added species planting. All 4 sites suffered from high numbers of exotic species. This continues to be a weakness in our restoration efforts.

VISUAL ASSESSMENT

Although prairie landscapes are regarded highly for characteristics that relate to science, wildlife, habitat, preservation, educational value, etc., the quality enjoyed by most people is probably that of visual aesthetics. Restorations are often judged visually with little concern for biological composition. Since continuing restoration efforts will need wide support, it seemed important to define what people expect to see when viewing a prairie.

After examining descriptions of natural prairies (available information is about natural rather than restored prairies), written by people with and without scientific perspective, I determined that 3 visual elements were consistently mentioned: grasses, flowers and open space. I concluded that the visual semblance of a native prairie could be recaptured in a planting dominated by finely textured grasses and accented by aggregations of forbs (flowers) that are set against the horizon. This admittedly simplistic definition provides a standard against which the visual quality of a restoration can be measured.

To assess visual elements in terms of quality, some landscape architects deal with 3 basic concepts: unity, memorability and intactness (Jones 1978). These 3 qualities were defined in terms of prairie landscapes as follows:

1. Unity is achieved by fine *texture* and seasonal *color* of dominant grasses.
2. Memorability is a result of medium to coarse *textures* and accen-

TABLE 2. Biological assessment applied to case studies. For explanation, see text.

	Sites (and dates of establishment)*			
Species categories	SH (1978)	PI (1976)	DD (1973)	BD (1972)
1. Planted (+)	+9	+5	+7	+13
2. Volunteered (−)	−19	−11	−14	−17
3. Annual/Biennial (−)	−7	−2	−2	−4
4. Perennial (+)	+21	+14	+19	+26
5. Native to Prairie (+)	+15	+10	+14	+21
6. Exotic to Prairie (−)	−13	−6	−7	−9
	+45	+29	+40	+60
	(54%)	(60%)	(63.5%)	(67%)
	−39	−19	−23	−30
	(46%)	(40%)	(36.5%)	(33%)

* SH is Spring Hill; PI, Pike Island; DD, Doug Dayton residence; and BD, Bruce Dayton residence.

TABLE 3. Visual assessment applied to case studies. For explanation, see text.

	SITES (AND DATES OF ESTABLISHMENT)*			
BASIC VISUAL QUALITIES	SH (1978)	PI (1976)	DD (1973)	BD (1972)
1. Unity				
Vegetational texture	3	3	3	3
Vegetational color	5	3	5	3
Subtotal	8	6	8	6
2. Memorability				
2. Memorability				
Contrast in texture	2	−3	0	4
Contrast in color	4	1	3	5
Spatial quality	1	1	1	0
Subtotal	7	−1	4	9
3. Intactness				
Presence of woody vegetation	−1	−2	−3	−4
Presence of exotics	−3	−1	−2	−1
Subtotal	−4	−3	−5	−5
Total of Subtotals	11	2	7	10
Divided by 3 Qualities	+3.7	+0.7	+2.3	+3.3

* SH is Spring Hill; PI, Pike Island; DD, Doug Dayton residence; and BD, Bruce Dayton residence.

ting *colors* of *forbs* through the seasons. Memorability is also a result of the *setting*, a kind of spaciousness associated with prairies of long past.

3. Intactness is secured by *limited intrusion* by exotic plants that signal a disturbance to the prairie landscape.

From these criteria, the assessment form was derived. Reactions to the visual landscape of a restoration are evaluated on a scale of 5 to −5. A total score is then calculated for comparative purposes.

When the technique was used on the 4 case studies, the oldest planting, Bruce Dayton's residence, ranked second (Table 3). It lost points in unity because planted forbs overpowered grasses; in memorability because the spatial quality was claustrophobic; and in intactness owing to woody invasion, all problems that could be improved by man. The youngest site, Spring Hill, showed the highest quality. Unity was strong thanks to the dominant grasses. A lack of intactness, due to pioneer weeds, should diminish with fire management. Pike Island stood out as achieving the least semblance of prairie.

DISCUSSION

In combination, the biological and visual assessments allow relative judgments of success in restorations. Further study may improve their usefulness. Both described the Pike Island level of success as a reconstruction more accurately. Both were more discriminating between levels of success among the remaining 3 sites that were rated equally in the Howell method. Both were easier to apply.

At this time, these techniques have value in (1) consuming minimal time, (2) requiring minimal biological knowledge, (3) eliminating the need for detailed records required in scientific comparison, and (4) being relevant to our simplistic planting goals rather than to the production of native prairies.

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USE OF OAK WILT TO CONTROL OAK INVASION OF PRAIRIE

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Abstract. Oak barrens, consisting of sand prairie or sand barren vegetation with widely spaced black oaks, were a type of savanna common in presettlement southern and central Wisconsin on sandy soils. In the University of Wisconsin Arboretum a 4-ha remnant which had been grazed until 1940 rapidly developed into thickets of small oaks (*Quercus velutina* × *ellipsoidalis*) under management which included infrequent burns and protection from grazing. In an attempt to control this invasion and restore the prairie understory, nearly 10,000 small oaks in the area have been inoculated over a 4-year period with *Ceratocystis fagacearum*, the fungus which causes oak wilt. Stringent precautions were taken to prevent spread to trees beyond the experimental area. In general, at least 90% of the inoculated trees developed the disease, which is fatal to oaks in the black oak group. Inoculations were most effective when performed soon after leaf expansion, in early June. Inoculation of 3 shoots versus 1 shoot per plant did not increase the infection success sufficiently to justify the increased labor. The rate of spread from inoculated individuals to nearby neighbors was too slow to aid in control, making it necessary to inoculate each individual. Oak wilt is an effective biological control suitable for areas which can be safely isolated and which are small enough to allow a labor-intensive procedure.

INTRODUCTION

Woody invasion of prairies is usually controlled with fire, cutting, or herbicide. Biological control is seldom a possible alternative because of the lack of appropriate parasites or predators. However, the troublesome invasion of a small savanna in the University of Wisconsin Arboretum by thousands of young oaks provided an opportunity to evaluate a well-known disease, oak wilt, as a biological control.

The experimental site, approximately 4 ha in size, lies on the south and west slopes of a knoll of sandy glacial deposits. The present vegetation is a remnant of a presettlement oak barren. The large open-grown trees as well as the abundant smaller ones are mainly a hybrid of 2 species which do well in sandy soil: black oak (*Quercus velutina*) and Hill's oak (*Q. ellipsoidalis*). A few bur-oaks (*Q. macrocarpa*) are also present. Where the prairie understory still exists it is dominated by little bluestem (*Andropogon scoparius*) and needle grass (*Stipa spartea*). Before acquisition by the Arboretum in 1940, the area was grazed (and possibly burned) enough to prevent forest invasion. Some prairie plants survived this agricultural period, and people who visited the area in the 1940s and early 1950s remember striking displays of prairie flowers, particularly lupine (*Lupinus perennis*).

Arboretum management of the area is not well documented, but apparently some burning, cutting, and (for a brief period) herbicide were used to attempt to keep at least part of the area open. By the early 1960s the problem of invasion by young oaks was severe, and when this experiment began in 1977, only small patches of prairie were free of young oaks. Groves of multiple-stemmed saplings 1-3 m tall with densities as great as 3 or more per m^2 covered much of the area. Clearly the management practices of the past 37 years had not been effective in preventing invasion by forest species. After experimenting unsuccessfully with moving and repeated hand-cutting in 1975-76, I turned to oak wilt as a possible alternative.

Oak wilt is caused by the fungus *Ceratocystis fagacearum*. It is fatal to oaks, especially those of the black oak group, and has caused substantial mortality in southern Wisconsin oak woods. The fungus can move from an infected to a healthy tree through root grafts. Insects attracted to the sweet-smelling fungal mats beneath the bark of infected trees may carry the fungus to fresh wounds in a healthy tree. The fungus is easy to grow in culture and susceptible oaks can be infected readily by inoculation. The idea of using oak wilt as a biological control is not new. French and Schroeder (1969) of the University of Minnesota showed that using oak wilt is as economical as using herbicides for eliminating oaks competing with pine plantings.

METHODS AND MATERIALS

After the decision was made to try to rid the area of oaks by using oak wilt, precautions were needed to prevent spead of the disease into adjacent oak woods (and the wooded lots of our neighbors). Consultation with James Kuntz of the Plant Pathology Department, University of Wisconsin, identified 3 main precautions:

(1) The organism used should come from diseased oaks in the immediate area to prevent introducing a new and possibly more virulent strain.

(2) Spread through root grafts to adjacent areas should be prevented by using a root cutter to cut all roots to a depth of 1.2 m between the experimental area and adjacent areas which had oaks.

(3) The experimentally infected oaks should be cut and burned after they die to prevent spread by insect vectors.

Because of the large numbers of oaks to be inoculated, I used the first series of inoculations to study 2 questions of efficiency: (1) If an individual has multiple shoots, is it necessary to inoculate more than 1 shoot? (2) If trees are close together, can spread of oak wilt though the roots reduce the number of inoculations needed? To answer the first question, experimental plots were set up in which up to 3 shoots per plant were inoculated; in other plots only 1 shoot per plant was inoculated. To answer the second question, a plot was set up in which the nearest individual to each inoculated individual was not inoculated.

Inoculation consisted of placing on the stem 3 drops of a water suspension of the fungus culture, then cutting through each drop with a razor blade. The cuts were observed long enough to be sure that the drop was drawn into the stem. Inoculation was done in June. Observations of infection incidence were made in August or September.

RESULTS AND CONCLUSIONS

Inoculated oaks usually showed wilt symptoms within 2 weeks. Some produced new basal shoots 1 or even 2 years after the infection had killed the tops, but these shoots also wilted.

Infection rate was slightly higher in the group receiving up to 3 inoculations (99.3% versus 95.3%) (Table 1). The fungus readily spread from inoculated to non-inoculated shoots, although multiple inoculations resulted in complete wilting of 55.6% of the individuals in that group after 90 days compared with 32.8% in the group inoculated on 1 shoot only. Since we were less interested in the rate of spread than in the end result, we adopted a general procedure of single shoot inoculations, except for very large multiple-stemmed individuals which received 2. French and Schroeder (1969) also concluded that multiple inoculations were unnecessary. In 1977, 1978 and 1979, I recorded infection incidence for nearly 1200 individuals inoculated under this procedure. The incidence varied from 99% to 90%, with the higher percentage resulting from inoculations made in early June, and the lower ones from those in late June (Table 1). Drake et al. (1957) also reported higher amounts of infection from early inoculations, noting that formation of summer wood may increase resistance.

TABLE 1. Percent infection of oaks inoculated with *C. fagacearum.*

Number individuals	Date inoculated	Days after inoculation	Individuals infected (%)	Individuals with 50% infection (%)	Individuals with 100% infection (%)
183*	6/21/77	90	95.3	59.4	32.8
134**	6/21/77	90	99.3	83.7	55.6
130***	6/29/77	85	90.0	60.0	33.1
196	6/1/78	79	99.0	97.5	53.6
305	6/6/79	69	99.0	83.6	33.8
291	6/21/79	54	96.2	77.7	2.1
239	6/25/79	50	90.4	31.0	2.1

* 1 shoot per individual inoculated.

** 3 shoots per individual were inoculated, unless fewer were present.

*** In this and all remaining groups, 1 or 2 shoots per individual were inoculated, depending on size of individual.

As in the previously cited work by French and Shroeder, there was very little spread between the inoculated oaks and adjacent non-inoculated oaks. After 2 years, only 6 of the approximately 130 non-inoculated individuals had wilt symptoms; after 3 years the total was 19. Mean distance from a non-inoculated, infected tree to an infected tree was 1.2 m the first year and 1.1 m the second year. Mean distance from a non-infected tree to the nearest infected tree was 1.0 m. Thus distance from an infected tree was not a good prediction of likelihood of spread, and spread through root grafts was insufficient to be helpful in the eradication program.

To date, over 10,000 small oaks have been inoculated. The prairie response is best where trees were less dense, or where there were intermittent efforts at clearing in the past, although even sections where trees were dense have a few prairie species. To help prevent re-invasion by oaks we will follow a rigorous burn schedule. In addition, we have begun to remove a row of oaks in a former fencerow which extends along the south and west boundaries of the knoll. These oaks provide both a seed source and tree-favoring amelioration of climate.

In conclusion, the experiment has demonstrated that oak wilt can be successfully and safely used as a biological control of oaks in sand prairie. Because of its specificity, there are no adverse effects on prairie species present. However, because it is labor intensive and requires strict safety precautions, use of this approach may be limited.

ACKNOWLEDGMENTS

James Kuntz, Departments of Forestry and Plant Pathology, University of Wisconsin, Madison provided valuable advice throughout the project, and arranged for growth of the oak wilt cultures in his laboratory. David French, Department of Plant Pathology and School of Forestry, University of Minnesota, St. Paul generously shared his experience and his enthusiasm for oak wilt as a biological control. I was grateful also to the many University of Wisconsin graduate students, faculty members, and Arboretum crew who helped to carry out the 10,000 inoculations.

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PRAIRIE STATE PARK: ENHANCING VISITOR EXPERIENCE THROUGH INTERPRETATION

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Abstract. Prairie State Park is owned and administered by the Missouri Department of Natural Resources and was acquired in 1980 with the aid of The Nature Conservancy. Located in Barton County, it will be managed to restore, preserve, and interpret southwest Missouri's tallgrass prairie.

The DNR's goal is to expand Prairie State Park up to 3,500 acres encompassing over 3,000 acres of prairie landscape. Currently, much of the acreage varies from pure prairie to a mixture including non-native species. Restoration of the prairie ecosystem will include the re-introduction of bison. Interpretation of this ecosystem, will provide visitors with an impression of the vastness of the "sea of grass" that was once Missouri's tallgrass prairie.

This paper addresses the facility and its recreational developments, and the methods of interpretation that will be used to achieve the desired visitor experience and elevate public awareness.

INTRODUCTION

Prairie State Park is owned by the Missouri Department of Natural Resources, and was acquired with the assistance of The Nature Conservancy. It is located near the town of Liberal in Barton County in southwestern Missouri.

Prairie State Park is 745 ha in size, and will grow to over 1,400 ha if all land identified in the purchase unit can be purchased. The park is part of the Osage Plains Natural Division of Missouri (Thom and Wilson 1980) and is one of the larger prairie remnants left today (Fig. 1). Barton County was 86% prairie at the time of settlement "according to presettlement records." Today the county is estimated to have 4% prairie left with Prairie State Park representing approximately 10% of that.

The following natural communities occur at Prairie State Park: dry prairie, dry-mesic prairie, mesic prairie, wet-mesic prairie, mesic forest, wet-mesic forest, wet seeps, and permanent streams. All lie over a mantle of Pennsylvanian shale and sandstone. Prairie communities predominate and include the mid- to tall grasses such as *Andropogon gerardii, Panicum virgatum, Andropogon scoparius, Sorghastrum nutans,* and *Spartina pectinata.* The forest communities in the park have come about through successional invasion along the larger permanent streams. In addition the park also contains a headwater stream of superb quality.

In addition to being a significant prairie remnant, the park fills a gap in the park system's goal of preserving representatives of Missouri's major landforms and communities.

PURPOSE OF THE PARK

The purpose of Prairie State Park is to maintain and restore the native tallgrass prairie ecosystem as it was in the 1840s when settlers first came to

TABLE 1. Interpretative plan for Prairie State Park.

INTERPRETATION SITUATION	INTERPRETATIVE SOLUTION
1 April-31 May	
A time to build park attendance. Although the weather is cool and pleasant, hazards due to controlled burns may develop. Schools are in session and it is a time when teachers desire to take their classes on field trips.	Develop special, highly publicized walks or special events such as spring wildflower walks, special programs showing historical significance of this type of management, stressing safety precautions. Programs on the ecological aspects of the prairie, stressing complexity and interactions of organisms so that the student may better understand the prairie; relying heavily on participant involvement.
1 June-Mid-July	
The weather is now quite pleasant and not a factor or even an aid to get visitors in the park. The visitor is looking for a place to go to enjoy the new wonders of the growing season.	Provide for short and long walks stressing wildflowers and birds. At this this time begin sunset walks.
Mid-July-15 September	
The weather is now very hot and uncomfortable during the day and most visitors will not be willing to do many activities in the hot sun. A time of low attendance.	Sunset walks, star programs, and creek walks are desirable. Day activities will be kept short and emphasize the prairie community with its spectacular forbs and now blooming grasses.
15 September-1 December	
The weather is again comfortable and visitors are again out looking for things to do. Schools are back in session and many special interest groups are again meeting after a summer off.	Longer prairie walks will be provided stressing how the prairie appeared to early settlers. The ecology of the tallgrass prairie with its complexity and species interaction will be stressed.
1 December-1 April	
A period of low attendance as the weather can be quite bad. The days are very short so most visitors do not want a long program.	Develop short winter walks to see winter birds and other sights. This is the time to build next season's attendance by presenting programs about the park and prairie to schools and civic organizations.

Barton County and through interpretation educate the public about tallgrass prairie. It will become increasingly important as a bench mark with which to compare man's impact on surrounding area, and a natural historic landmark of man's past—an island of beauty amid man's development.

INTERPRETIVE PLAN

How can the visitor leave with an understanding and appreciation of Prairie State Park? The answer is proper interpretation by the staff. To aid the park staff an interpretative plan has been developed for Prairie State Park. It contains seasonal characteristics that affect interpretation for the anticipated park visitor. It is designed to improve interpreting skills for the park visitor by identifying time periods of floral display, animal activity, etc. during the calendar year and the types of anticipated visitor activity best emphasized at each time (Table 1).

Most of the plan hinges on small numbers of visitors per park naturalist to allow the most enjoyable experience. Publicity is necessary to attract visitors to the facility, for it is located far from a metropolitan area. Therefore, presentations to schools and civic groups are very important. Articles in newspapers and specific interest group newsletters are essential if the public is to know about and visit the park.

STATUS OF THE PARK

We have had limited opportunities to implement this plan as the park has only been open since 27 June 1982. The park has been involved in special interpretive events involv-

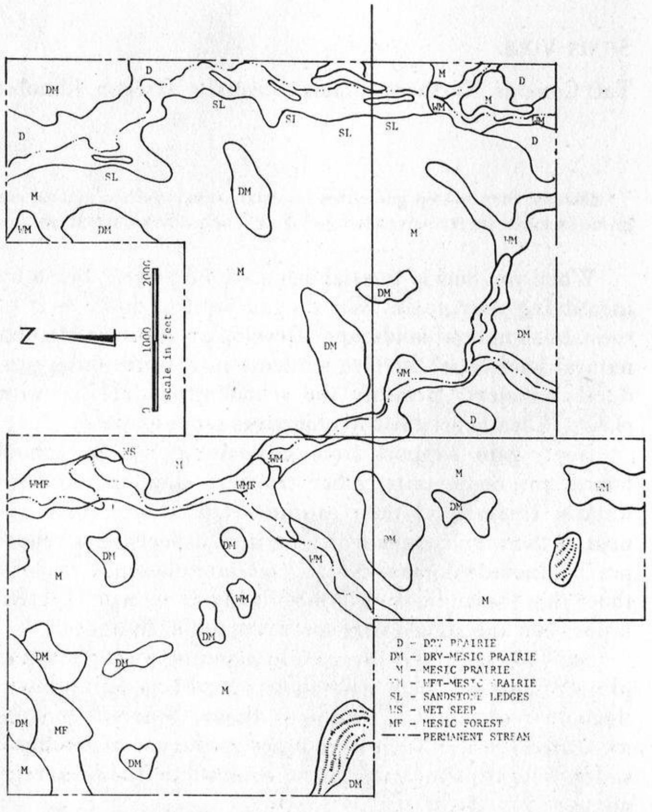

FIG. 1. Natural communities of Prairie State Park, Barton County, Missouri.

ing other state parks and has hosted its own special program.

Before the park was open we participated in Missouri State Park's Spring Wildflower Walks. This statewide publicity was supplemented by articles written by the park naturalist that appeared locally.

The special event of the park dedication was held on 27 June 1982, in conjunction with Governor Bond's proclamation of Missouri Prairie Day. The dedication served as an opportunity for interpretation of ther prairie to visitors. In addition to the speakers and the formal dedication ceremony, naturalists from nearby state parks led walks, explaining the purpose of Prairie State Park and identifying fauna, flora and other natural history features.

A living history demonstration was designed so that visitors could walk to a reconstructed trapper encampment (the trappers were going west to harvest another crop of furs for sale in St. Louis). They explained the hardships of the prairie and demonstrated survival skill. Visitors who chose not to walk to the camp could be carried there by a replica Conestoga wagon drawn by Missouri mules. These activities made the day very enjoyable for the visitor.

Increased attendance this summer (1982) was directly linked to the Spring Wildflower Walks and/or the Park Dedication. The publicity accompanying these events was important in attracting new visitors to the park during subsequent weeks. The park also participated in 1 other state-wide event, an eclipse watch during the early morning of 6 July 1982.

Visits to a new remote park such as Prairie State Park must rely on publicity. Park participation in state-wide and regional events has been effective in increasing park visitation.

The interpretive services offered at Prairie State Park describe how the prairie, in yielding to civilization, has become an endangered community (landform) in Missouri. The maintenance of Prairie State Park will ensure that some of the rolling prairie that once was a very significant part of Missouri's heritage will be here for future generations.

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SCHOOL PRAIRIES

SONIA VOGL

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Abstract. Step-by-step guidelines for establishing a school prairie are given. Included are recommendations for student involvement and use.

When you decide to establish a school prairie, begin by identifying your goals. Why do you want to do it? Is it to reestablish natural landscape? Develop an appreciation of a natural landscape? Involve students in a worthwhile, productive project? Beautify the school grounds? Use with classes? Clearly established objectives are essential.

Next, gain support from administrators, the school board, the community, other teachers, and maintenance workes. Understand their attitudes and values, then approach them and explain the positive aspects of a school prairie. Include the major goals you have chosen, especially those that the audience will most likely agree with. Presentations can and should vary according to the audience.

Students should be involved in planning throughout the project. This will help gain their support as well as help them to feel that the prairie is theirs. Students can be motivated through such techniques as the use of readings, slides, field trips to prairies, and contests to find local remnants.

Funding is essential. The amount of funds needed will depend on the size of the prairie and the method of obtaining seeds or stock, through purchase, through class collections, or through donations of materials.

Next, decide on the size of the prairie garden. Will it provide a feeling of the expansiveness of the prairie, or will it initially be small for easy management? The first prairie we planted consisted of several small plots, totaling about 800 square feet. A small plot allows greater possibilities of success; a very large plot could easily get out of hand. Be sure you have enough manpower to plant and maintain the size you decide on.

Where will the school prairie be located? In front of the school for decorative purposes? In the courtyard, where it can be protected? Outside your window, where you can observe it, protect it, and use it with classes?

The actual planting is the next step. Soil conditions govern the types of plants you can grow. A list of species adapted to wet, dry, or medium conditions appears in *Prairie Primer* (Stan Nichols and Lynn Entine, University of Wisconsin Extension, 1535 Observatory Drive, Madison, Wisconsin 53706). You will probably want color throughout the growing season: in spring and fall for your classes, and in summer to please the neighbors. Calculate the number of plants the plot will accommodate. Taller plants should be placed toward the rear of the plot. This will assure that new growth and bloom is always in the foreground.

Weigh the advantages of seeding vs. planting before choosing a method. Seeding is cheaper but starting with plants will provide quicker bloom. It will also make weeding easier, since you will know exactly which are prairie plants.

Exercise care in obtaining seeds or plants. Both should come from local sources. If you plan to gather seeds, do so under the supervision of a knowledgable dealer. Plants should be purchased from a reputable dealer. Do not purchase from those who collect from high-quality remnants, who sell seed from distant locations, or who sell weedy plants. Get a list a dealers; check their reputations with the Nature Conservancy or state Department of Conservation or Natural Resources.

Good planting directions can be found in *The Prairie Garden* (J. Robert Smith, The University of Wisconsin Press, 114 North Murray Street, Madison, Wisconsin 53715). Plant and maintain according to directions, and the school prairie may be a great success.

Use the prairie with your classes. Biology classes can study plant identification and the structure of plants, especially grasses. The prairie ecosystem including animals can be compared to other ecosystems. Study comparative growth patterns of prairie plants and Eurasian weeds. This is especially striking in spring. In fall, study seed dispersal.

Social studies classes can use the prairie for American history units and units on other grasslands throughout the world. Walk through the prairie; sit in it; try to imagine how the pioneers felt. Read selections on life in the prairie while actually in the school prairie. Study the uses of prairie plants. Dig into the soil to understand the meaning of breaking the prairie sod. The history and development of many cultures can be related to their heartlands (the breadbaskets of the world).

Language can include creative writing and poetry, and can be successfully incorporated into social studies.

Art classes can sketch plants and record color variations and distributions. Physical education and movement classes can imitate the motion of grasses in the wind. Music classes can compose tunes and harmonies to express the feel of the prairie.

Math classes can calculate plant density. Growth rates of prairie plants can be measured, recorded, and compared to growth rates of plants in other grasslands. Root: shoot ratios of prairie plants can be compared to those of trees and lawns.

Finally, to help insure long-term preservation, make as many persons as possible aware of the prairie. Take groups to observe. Make presentations to community organizations. Make it a point of community pride.

ABSTRACTS OF OTHER PAPERS PRESENTED AT THE EIGHTH NORTH AMERICAN PRAIRIE CONFERENCE

Below are included abstracts of all presentations from formal paper sessions not included in full elsewhere in the *Proceedings*. Information on papers in print or in press elsewhere is given, where available.

LIMESTONE GLADES OF HARRISON COUNTY, INDIANA.[1]

James R. Aldrich, John A. Bacone, and Max D. Hutchison, Indiana Natural Heritage Program, Department of Natural Resources, 612 State Office Building, Indianapolis, Indiana 46204, and Division of Nature Preserves, Department of Natural Resources, 601 State Office Building, Indianapolis, Indiana 46204, and Belknap, Illinois 62908

Limestone glades are relatively small natural openings occurring in the forest in southern Indiana. These openings are dominated by prairie species and are remnants of a community type that was apparently more common and widespread in presettlement times. They are found on south- and west-facing slopes, on very thin soil with bedrock exposed, and have apparently been much reduced in size due to the suppression of natural wildfires. Inventory efforts located a number of potential high-quality glades, a plant community type previously undescribed in Indiana. Inventory procedures included examining maps and photos, aerial surveillance, and numerous ground checks. Four high-quality glades are described and species lists presented.

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[1] In press, *Proc. Indiana Acad. Sci.* 91.

UPPER AIR CIRCULATION AND THE PRAIRIE-FOREST ECOTONE IN SOUTH-CENTRAL CANADA.[1]

DeWitt H. Braud and Jay R. Harman, Department of Geography, Michigan State University, East Lansing, Michigan 48824

The relationship between summertime air flow patterns at the 500 millibar level and the location of the prairie-forest ecotone in south-central Canada was investigated. Surface data collected from approximately 100 stations in southern Saskatchewan and Manitoba, North Dakota, western Minnesota, and eastern South Dakota included dates of 0.1 inch or more precipitation and observed maximum and minimum temperatures for June through August, 1962-1971. Each day in this period was also classified according to whether the prevailing upper-level air flow was from the northwest, west, southwest, or was variable across the region. Daily temperature and precipitation frequencies were then calculated and mapped by each flow category.

Isolines of precipitation frequency closely paralleled the ecotone only under northwesterly flow, when values northeast of the ecotone were up to 150% to 300% higher than those southwest of it. Southwesterly flow provided a distribution of precipitation events unrelated to the ecotonal position. Under northwesterly flow, isolines of mean maximum daily temperature most nearly paralleled the ecotone, with higher temperature to the southwest, and the highest mean temperatures were observed areawide. Of the 4 flow categories, those classified as regionally "variable" were the most frequent; a number of different specific patterns were contained within this category. Of the discrete patterns recognized, including those lumped into the "variable" category, northwesterly flows were the most frequent. Approximately 30% of all days in both July and August, the warmest months, fell into this group.

We conclude that the modal summertime circulation patterns in this region lead to a spatial distribution of climatic stresses consistent with the location of the ecotone. As a result, we suggest that the ultimate origin of the ecotone may lie in the cumulative effects of daily stresses rather than in infrequent, extreme, catastrophic events.

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[1] Harman, J.R., and D. H. Braud. 1975. Flow patterns at the 500 mb. level and the prairie-forest ecotone in Canada. *Mich. Acad.* 7:347-356.

AN ORDINATION OF MICHIGAN GRASSLAND RELICTS.[1]

Kim Alan Chapman,[2] Department of Biology, Western Michigan University, Kalamazoo, Michigan 49008

At the northeast edge of the prairie peninsula, Michigan grassland is more influenced by the deciduous forest which surrounds it than is grassland in Illinois and farther west. In the past 2 decades several papers dealing with relicts of Michigan's grassland communities have assumed, but for the lack of a few species, a direct parallel with western prairie.

To produce a clearer picture of Michigan grassland types, I visited 53 grassland relicts and 18 fens over 3 seasons to compile species lists. Many of these were augmented by lists from theses, articles and, most importantly, notes kept by other Michigan field workers. Nine additional stands were added from the literature and others' field notes. In 1981 I tested soil *p*H, texture, and water-retaining capacity at 48 sites. Other information (dominant species, edge communities, aspect, % slope, etc.) was recorded at every site visited. Also, soil survey maps were consulted to determine soil type beneath the relicts and the soils of the region in which each was located. At 15 "benchmark" stands, frequency and dominance were determined using randomly thrown cross-quadrats. These data were on hand for 5 additional stands.

I analyzed the floristic data with a computer ordination procedure. Complete species lists, rather than cover or frequency, were used because uncommon, but constant and modal, species might contribute to a characterization of a community as much as other factors. The Bray-Curtis ordination method (*Ecol. Monogr.* 27:325), as implemented by Beals (*Wilson Bull.* 72:156), was chosen because the formulas are simple, and computer algorithms for them could be constructed easily. Criteria for the selection of axis endpoints were roughly those of Swan and Dix (*J. Ecol.* 54:13), but modifications were made; chief among them was a way for dealing with the problem of stand-to-stand differences in species number. Sixty-two grassland relicts were used in the ordination. Four fens for which good data exist were added to this to discover part of the relationship of fen to prairie. No other fens were included because I thought that fen was a fairly uniform and predictable community in Michigan.

Coordinates for stands along 3 dimensions were produced and a model constructed. This did not account for all the variation between stands. A fourth dimension revealed additional relationships between stands, but was not included in the model. Three clusters of stands appeared in the model, corresponding to upland grassland and 2 types of lowland grassland. Between these clusters lay stands of intermediate nature. Correlated with the upland relicts was an acidic sandy loam or loamy sand of low to moderate water-retaining capacity. Associated with one of the wetland types was, in most cases, a neutral loam or silt loam having moderate water-retaining capacity and with the other wetland, a moderately alkaline sandy loam or loam of moderate water-retaining capacity. Fens were situated on neutral to slightly alkaline muck of a very high water-retaining capacity.

Most of the upland stands lay in regions forested by oak and were surrounded by, or contained, oaks. Settlers' accounts, descriptions in early soil surveys, and present soil conditions indicate that these relicts represent the understory of former oak openings, and as such are not "true prairie," but rather woodland prairie. The first wetland type resembles lowland prairies of Illinois and points west, and is found in the limits of the prairie peninsula's extension into Michigan, but not in far southeast Michigan or in the Saginaw Bay region. The second wetland type is restricted to southeast Michigan and the Saginaw Bay region.

The ordination detected trends in the upland stands beyond those obvious ones in the 3-dimensional model. In the early stages of endpoint selection, I saw that certain collections of stands were pulled consistently toward an endpoint if one of their members was selected as the endpoint. These "nodes" in the upland cluster are visible to some degree in the model and could be distinguished as additional grassland types. In an expanded classification, the grassland types of Michigan would be

1. Dry Sand Prairie;
2. Woodland Prairie (dry-mesic), the upland group of stands with soil characteristics described above;
3. Mesic Sand Prairie;
4. Hillside Prairie (dry);
5. Mesic Prairie, in the sense of Curtis (*Vegetation of Wisconsin,* 1959);
6. Wet Prairie, in the sense of Curtis, the first wetland type described above;
7. Eastern Wet Prairie, the second wetland type described above;
8. Fen.

Dry-mesic and Wet-mesic Prairie, as understood by Curtis, and Eastern Wet-mesic Prairie could also be recognized but, as is the case for Mesic and Mesic Sand Prairie, so few examples of these types now exist in Michigan that they could not form clusters or nodes in the ordination.

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[1] This research was partly funded with a Graduate Research Grant from the Graduate College, Western Michigan University.

[2] Current address: Michigan Natural Features Inventory, 5th Floor Mason Bldg., Box 30028, Lansing, MI 48909.

MEAN SUMMER CLIMATE AND CIRCULATION PATTERNS INFLUENCING THE PRESETTLEMENT FOREST-PRAIRIE ECOTONE IN THE SOUTH-CENTRAL STATES.[1]

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Drier conditions westward are generally seen as most important to the central states ecotone, but no single daily weather variable has previously been shown to be a controlling factor. In addition, features of the general circulation which cause the unequal distribution of moisture in the central states have not been explicated. Plant physiologists have demonstrated that vapor pressure deficit (VPD, vapor pressure gradient from leaf to atmosphere) is an influential factor on photosynthesis. In general, grassland species are least affected by high VPD, and broadleaf trees are most affected.

A mean summer VPD gradient exists across the location of the southern ecotone. Summer days on which the VPD gradient is strongest are days on which mid-tropospheric windflow patterns are identical in form to the long-term mean summer windflow pattern. It is, therefore, frequent occurrence of the most common weather patterns which cause a climatic situation favorable to the presettlement distribution of forest and prairie. It is possible that a more frequent occurrence of the modal mid-tropospheric windflow pattern could cause eastward expansion of grassland climate.

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[1] 1983. *Physical Geography 3:148-159.*

EARLY STAGES OF PRAIRIE RESTORATION ON A 3-ACRE FIELD IN CENTRAL ARKANSAS.[1]

Donald Culwell and Robert Wright, Biology Department, University of Central Arkansas, Conway, Arkansas 72032

A plot of land on the UCA campus has been designated as a permanent Nature Reserve, to remain much as it is with woods and open, grassy fields for educational purposes. The 3-acre open field is good for prairie restoration, since the area has not recently been under cultivation. *Andropogon gerardii, A. scoparius, Sorghastrum nutans, Panicum virgatum, Liatris pycnostachya, Eryngium yuccifolium, Rudbeckia hirta,* and *Helianthus* sp. are examples of the native plants frequently occurring here. Other plants typical of prairie remnants in Arkansas occur less abundantly. Vegetation monitoring has included compiling a species list and gathering quantitative data on the density, dominance, and frequency of sampled species at several times during the growing season. Restoration has involved elimination of some encroaching woody species, burning, and a program of seed collection, sowing, and transplant operations.

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[1] Wright, R., and D. Culwell. In press. Early stages of prairie restoration in a 1.5-hectare Field in Faulkner Co., Ark. *Proc. Ark. Acad. Sci.* 35.

POSITION AND HOLOCENE HISTORY OF THE PRAIRIE BORDER IN MINNESOTA.

Edward J. Cushing. Department of Ecology and Behavioral Biology, University of Minnesota, Minneapolis, Minnesota 55455

At the time of settlement by Euro-Americans, the transition across Minnesota from continuous grassland to continuous deciduous forest was relatively abrupt, from a few m to a few km broad. Scrubland and parkland of *Quercus* and *Populus* occupied the transition. The position and abruptness of the border was strongly correlated with topography and the location of natural firebreaks, indicating that fire was the most important causal agent.

Mapping of pollen percentages at 1,000-year intervals through the Holocene permits estimation of the changing position and nature of the border. Prairie was absent in the upper Midwest before 10,000 years ago, but it replaced forest rapidly thereafter, and by 8,000 years ago the edge of continuous forest was about 150 km east of the present position. Between those 2 positions, areas with low relief and few bodies of water such as outwash plains and till plains were occupied by continuous prairie. Rugged moraines were occupied by scrubland, parkland, or perhaps savanna. After 6,000 years ago, the forest edge moved westward to its present position in an irregular way. Apparently the canopy closed first in the areas of rough topography. These areas of closed forest may then have reduced the frequency of fire on inliers of prairie sufficiently that trees could invade and forest develop. This process was still in progress as recently as 500 years ago in the Big Woods region of central Minnesota, but by then most of the areas of high local relief in the state had been occupied by forest. Thus the abruptness and stability of the prairie border in Minnesota may have been greater at the time of settlement than at any previous time in the Holocene.

GERMINATION, TRANSPORTATION, AND WINTER STORAGE OF IOWA PRAIRIE FORBS: SOME OBSERVATIONS.

Pauline Drobney, Biology Department, University of Northern Iowa, Cedar Falls, Iowa 50614

Automatic misters provide a source of humidity for surface-sown seedlings, which results in easy observation and rapid germination. Nearly all seeds that were germinated under this system germinated within 3-4 weeks. Transplantation of most of the 16 species tested did better if transplanted at the cotyledon stage rather than the 2-leaf stage. Young seedlings should not be allowed to become dry, and watering continues to be critical once the longer prairie roots develop. While underwatering can severely damage or kill a young prairie forb, overwatering quickly causes a surface algal growth and often death. Clay pots seem to be more desirable than peat pots or Jiffy 7's for transplanting. Field transplantation may be accomplished successfully at any time during the growing season, with mulching of grass clippings or wood chips being desirable for keeping weeds down and soil moisture up. Watering is essential at first. Overwintering may be accomplished in a cold room or a cool greenhouse; outdoor storage temperatures may be too severe for lightly protected potted prairie plants. Greenhouse-stored seedlings will begin to bloom far ahead of schedule, and many 4-6 month old seedlings planted in the field their first season will bloom the first year.

THE EFFECTS OF STRATIFICATION TIME ON THE GERMINATION RATE OF PRAIRIE FORBS.

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Seeds of the following species of prairie forbs were collected from local prairie remnants and a prairie restoration: *Amorpha canescens, Anemone cylindrica, Baptisia* spp., *Baptisia leucantha, Coreopsis palmata, Desmodium illinoense, Dodecatheon meadia, Echinacea pallida, Eryngium yuccifolium, Gentiana andrewsii, G. crinita, G. puberula, Geum triflorum, Liatris aspera, L. pycnostachya, Petalostemum candidum, P. purpureum, P. villosum, Silphium laciniatum, Veronicastrum virginicum,* and *Zizia aurea.* All seeds were collected in 1979 except for *Petalostemum candidum* and *P. purpureum* which included additional collections harvested in 1978. The 1978 and 1979 harvests were tested in spring 1980. In spring 1982, some species were retested from seeds harvested in 1980 and 1981. Extraneous material was removed from the seeds which were then divided into lots of 50. Legumes were scarified and all seeds were soaked 12 hours prior to stratification. Groups of seeds were stratified at approximately 33°F for 10, 8, 6, 4, and 2 weeks, 1 week, and 1 and 0 days. All groups were removed from the cold chamber simultaneously, sown on Pasteurized soil, and placed in a greenhouse under automatic misters.

Results indicated that the composites generally had a higher germination rate with 6-10 weeks stratification, while legumes germinated best with 4 or fewer weeks of stratification. Species were also analyzed according to their blooming dates. April to June bloomers seemed to require longer stratification, June to July bloomers showed no trend, while those blooming from July to August generally required lesser amounts or no stratification. One-year-old *Petalostemum* seed seemed less vigorous in initial growth than current year's seed, though not much different in percent germination. Because of very poor germination in the 3 species of *Gentiana* and in *Coreopsis*, they are considered special problems.

POST-BURN FLOWERING RESPONSE OF GRAMINOID SPECIES IN A WESTERN MINNESOTA TALLGRASS PRAIRIE. Bohdan Dziadyk, Department of Biology, Augustana College, Rock Island, Illinois 61201

Frequencies (based on occurrence in multiple 0.25-m^2 quadrats) and densities of flowering culms were determined for physiognomically important species of graminoids in the growing season following an October wildfire. The study area is a 490-ha remnant of native grassland in the Red River Valley in western Minnesota. Flowering response to the burn was analyzed at 5 sites representing distinct plant communities within the prairie. These included 1 upland or high prairie site, 2 mid-prairie sites, 1 low prairie area and 1 wet meadow site. *Andropogon gerardii* exhibited its greatest frequency (92.2%) within 1 of the mid-prairie sites, but its greatest flowering response (61.0 culms/m^2) was noted in the low prairie. *Andropogon scoparius* and *Sporobolus heterolepis* both had greatest frequency (82.8 and 93.8%, respectively) and greatest flowering response (51.5 and 103.5 culms/m^2, respectively) in 1 mid-prairie site. *Bouteloua gracilis* occurred only in the high prairie where it exhibited a relatively high frequency (76.6%) and flowering density (44.2 culms/m^2). *Spartina pectinata* had its highest frequency (65.6%) and flowering response (5.4 culms/m^2) in the wet meadow. The greatest frequency and flowering density noted for any 1 grass species was for *Muhlenbergia richardsonis* (98.4%, 116.3 culms/m^2); however, some species of *Carex* exhibited 100% frequency in several sites. Species distribution and flowering activity are related to soil moisture and other edaphic factors which vary along topographic gradients.

ENDANGERED AND THREATENED PLANT SPECIES OF SCHWAMBERGER PRESERVE, LUCAS COUNTY, OHIO.[1] Nathan William Easterly, Department of Biological Sciences, Bowling Green State University, Bowling Green, Ohio 43403

Of the 425 plant species observed within Schwamberger Preserve, 10 species (2.4%) are listed on Ohio's legal list of endangered species prepared by the Ohio Department of Natural Resources and 12 taxa (2.8%) are threatened or potentially threatened. Of the 23 taxa listed in this report, 11 species (47.8%) are originally from the Atlantic Coastal Plain. The location of the 5 plant communities within the preserve is governed by variation in water table depth rather than variation in soil *p*H. The future of Schwamberger Preserve as a viable scientific study area will be determined by management practices such as (1) acquisition of a buffer zone, (2) control of aspen thickets, and (3) maintenance of the existing excavations and creation of new ones to serve as specific study sites.

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[1] In press, *Ohio J. Sci.*

HYDROLOGIC CYCLE OF A LIMESTONE CEDAR GLADE IN SOUTH-CENTRAL MISSOURI.[1] Joseph A. Gates, Carl D. Settergren, Gray S. Henderson and J. John Krstansky, School of Forestry, Fisheries and Wildlife, University of Missouri-Columbia, Columbia, Missouri 65211

Analysis of 15 months of hydrographs and 1 year's time discrete water samples from 3 matched headwater catchments (0.30, 0.38 and 0.55 ha) on a limestone cedar glade with shallow soils (25 cm) and steep slopes (25%) showed unexpectedly that interflow is a major contributor to total storm runoff. Unlike those from most semi-permeable areas, storm hydrographs have steep ascending limbs, sharp peaks, and long tapering descending limbs.

During the 1981 water year (March 1981 to February 1982) 60 storms occurred ranging in size from 0.03-8.08 cm. Only 34 storms produced runoff and 14 storms accounted for 99.7% of all runoff. These 14 storms yielded 1.0 to 230 m^3. This was not an extreme event year. Runoff losses from single events never exceeded 50% on frozen soils or 33% on unfrozen soils. Seldom did losses exceed 25% and usually they were less than 15%. A 2-layered hydrologic model of a thin, highly permeable soil overlying a less permeable bedrock was more appropriate for the study site than an impermeable bedrock layer, which does not allow for deep seepage losses.

A water balance for the water year showed a 3 catchment average loss due to evapotranspiration (41.7 cm), runoff (11.5 cm), and seepage (36.1). This was 13%, 47%, and 40% of precipitation respectively. Little variation occurred among catchments.

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[1] Published, 1982, *in* Environmentally Sound Water and Soil Management (E. G. Kruse, C. P. Burdick, and Y. A. Yousef, eds.). American Society of Engineers, Irrigation and Drainage Division, New York.

ATMOSPHERIC CIRCULATION CONTROLS ON THE LOCATION OF THE PRAIRIE-FOREST TRANSITION ZONE IN THE UPPER MIDDLE WEST, U.S.A. John A. Harrington, Jr., Department of Geography, University of Oklahoma, Norman, Oklahoma 73019

The position of the prairie-forest transition zone in the western Great Lakes region is primarily a function of summer-season moisture stresses; ecophysiological studies indicate that this climatic parameter limits both seedling survival and growth of dominant species within the Deciduous Forest Formation. Potential evapotranspiration estimates, a surrogate for plant moisture stress, are used to identify individual days with a gradient in stress across the transition zone. Analysis of associated daily upper atmospheric wind-flow direction demonstrates that surface climatic conditions are linked through vertical motions to the atmospheric circulation; in addition, modal flow patterns aloft are associated with surface moisture stress gradients that probably generated and now reinforce the ecotone location. Research results indicating that most frequent upper atmospheric wind flow directions are related to environmental stresses that coincide with the prairie-forest transition imply that the phytogeographic boundary may be set by gradual accumulation of the effects of a frequently occurring stress pattern.

PHARMACODYNAMICS OF POISONOUS OR OTHERWISE HAZARDOUS PLANTS IN THE PRAIRIE COMMUNITY. Samuel B. Harper and Darrel G. Morrison, Department of Landscape Architecture, University of Wisconsin, Madison, Wisconsin 53706

The presence of potentially poisonous or otherwise injurious plants have long posed a threat to exploitation of this community for forage and grazing purposes. Man's popular enthusiasm for a return to nature creates a possible risk to those who might utilize prairie plants inappropriately. A brief introduction to the pharmacodynamics involved directs attention to potential hazards.

NINE-MILE PRAIRIE "REDISCOVERED": DOCUMENTING A 50-YEAR ECOLOGICAL RECORD OF AN EASTERN NEBRASKA TALLGRASS PRAIRIE. A. Tyrone Harrison, School of Life Sciences, Univ. of Nebraska, Lincoln, Nebraska 68588

Nine-mile Prairie near Lincoln, Nebraska is a 230-acre virgin tallgrass prairie with well-documented records on its native plants and animals. The original plant species list (Steiger 1930) has been annotated and its nomenclature updated. Flowering plant species were re-collected in 1979-80. Of the 345 species found by Steiger (277 native + 66 introduced), 173 native species + 50 introduced weeds were found in 1979 (a total of 223 species re-collected). In addition, 37 new native species, and 19 new introduced weeds are now found on Nine-mile Prairie (a current record of 281 species). Additional plant collections are needed. A time series of 8 historic photographs beginning in 1937 have been assembled from federal and state files to document land-use changes, old-field succession, woody shrub invasion, overgrazing, and drought effects. Vegetation changes based on these aerial photos are described. Quadrat data collected in 1980 were compared with the 1927-28 data of Steiger, and ongoing research and teaching projects and management plan were discussed.

THE BIOGEOGRAPHIC SIGNIFICANCE OF THE NATURE CONSERVANCY'S NIOBRARA VALLEY PRESERVE IN THE SANDHILLS OF NEBRASKA.

A. Tyrone Harrison, School of Life Sciences, University of Nebraska, Lincoln, Nebraska 68588

The Niobrara Valley corridor along the northern edge of the 20,000 square miles of Nebraska Sandhills Prairie has recently been recognized as having great biogeographic significance in understanding the post-Pleistocene development of the prairies and forests of the north-central Great Plains. This prairie river valley is a post-Pleistocene refugium for northern plant species at their southern limit on the Great Plains, for eastern deciduous forest species at their western boundary, and also for Rocky Mountain western species at their eastern limit on the Great Plains. The Niobrara Valley is the distributional limit for approximately 160 plant species.

The most striking feature of the Valley is the co-occurrence of 6 or 7 different vegetation types all within 1 or 2 miles of each other. Few areas of similar size in North America have this kind of habitat and floristic diversity. Most of the Nature Conservancy's 55,000-acre Niobrara Valley Preserve consists of the picturesque rolling Sandhills prairie. In addition western ponderosa pine forests, eastern deciduous forest biota, together with riparian forests and tallgass prairie meadows are all found within the valley. A unique northern boreal flora with paper birch trees (*Betula papyrifera*) is found on sheltered, north-facing slopes near permanent cool springs. Mixed prairie grassland occurs on the higher, dry, flat tablelands. The diverse topography, microclimates, geology, and soils have created an ecologically unique situation in the middle of the Great Plains grassland climate. Some species of birds, trees, and other plant species hybridize here at the edges of their respective ranges. This small but ecologically important biogeographic and evolutionary "natural experiment" is currently threatened by the construction of a 20-mile-long Bureau of Reclamation irrigation reservoir called the Nordem Dam Project (O'Neill Unit) of the Pick-Sloan Missouri Basin Program.

RE-ESTABLISHMENT OF A PRAIRIE TRANSITION OAK-HICKORY SAVANNA IN CENTRAL MISSOURI.

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Lincoln University and Mark Twain National Forest are engaged in an effort (1) to develop and refine techniques to re-establish prairie transition, oak-hickory savannas from off-site wooded stands and (2) to document this process through a gross ecological study. The area includes 75 acres of land determined from historical records, soil surveys, and understory flora as having originally been a prairie transition savanna. Remnant transition prairies are adjacent on 3 sides. Naturally occurring oak-hickory is interspersed with the study site, primarily on slopes. Through fire protection and improper grazing the site has been invaded by oak and hickory since 1817. Area perimeters were determined by changes in soil type and provide natural interspersion with wooded stands. Trees were removed through firewood sales with 5 to 30 selected trees left per acre. The resulting slash was burned. Control of oak and hickory sprouts is the major problem. Highly selective application of Krenite is used to control sprouts. Continued development will be by periodic burning and controlled grazing. Natural re-establishment of prairie plants should be enhanced by dispersal of seed from adjacent prairie remnants, from isolated plants within the area, and from dormant seed in litter and soil. No other treatments are anticipated. Ecological data are being collected on the study site and adjacent remnant prairies. Information on vegetation, insects, soil chemicals, soil temperature, soil moisture, small mammals, and weather is also being collected. Sample plots were established by soil series. A seed-bank study is underway to determine the quantity of prairie seed in litter and soils.

RESPONSE OF SELECTED PRAIRIE SPECIES TO DIFFERENT FERTILIZATION TREATMENTS ON IRON ORE TAILINGS.

Gretel E. Hengst and Darrel G. Morrison, Department of Landscape Architecture, University of Wisconsin, 25 Agricultural Hall, Madison, Wisconsin 53706.

Field studies utilizing predominantly native prairie species to revegetate iron ore tailing deposits at the Jackson County Iron Company mine near Black River Falls, Wisconsin, were initiated in the spring of 1979. Now, of moderate amounts of nitrogen and phosphorus, several prairie species provide effective vegetative cover in the difficult environment which exists on such deposits.

Four-m^2 plots, replicated 4 times, have been monitored in 1979, 1980, and 1981, to determine the response of a mix of 9 prairie species and 1 non-native annual on a total of 11 different fertilization treatments. Nitrogen was applied at the time of planting and at the beginning of the 1980 and 1981 growing seasons as ammonium nitrate at rates of 0, 88, and 175 kg/ha. Phosphorus was applied only at the time of planting as triple super phosphate at 0, 28, and 112 kg/ha. The various combinations of nitrogen and phosphorus applications constituted 9 treatments. Additionally, 2 rates of sewage sludge, 42 and 85 metric tons/ha, were tested, for a total of 11 different treatments.

In 1979, *Setaria* spp., the non-native annual in the seed mix, dominated the test plots, followed by *Elymus canadensis* and *Bouteloua curtipendula.* In 1980 and 1981, as expected, *Setaria* spp. diminished dratically, and the other 2 species have acquired greater numerical and visual importance. *Rudbeckia hirta* and *Monarda fistulosa* flowered conspicuously in 1980, the second growing season. *Lespedeza capitata,* in very limited numbers, reached flowering size in 1981.

Aerial foliage cover averages at the end of the second growing season were generally correlated with the rate of fertilizer application; e.g., 40% cover on plots with no nitrogen or phosphorus applied; 92% on plots receiving the low nitrogen application in combination with the high phosphorus treatment. Third year cover results were similar.

It is expected that vegetation composition will continue to change over time, as organic matter and nutrient supplies increase, creating an environment more suitable for invasion by other species.

PRAIRIE RESTORATION AND CONDOMINIUM COMPLEXES.

Douglas William Jaques, Briarwood Valley Arboretum, 3713 West Main, Kalamazoo, Michigan 49007

Condominium developers would attenuate the impact of their activities on the environment if they were to integrate prairie restoration into their land-management programs. Such an orientation would also tend to foster a wider acceptance of the land ethic and provide a concrete educational resource for nature appreciation.

A substantial literature currently provides condominium planners with a wealth of information on all aspects of prairie reconstruction, and commercial dealers offer at modest cost a wide selection of prairie grasses and forbs.

Prairie restoration offers the condominium developer a supremely cost-effective alternative to more traditional forms of landscaping. While the expense of initiating a prairie reconstruction may be comparable to the cost of establishing proportional areas of bluegrass, the maintenance expenditures for the prairie are but a fraction of the funds required to maintain traditional lawns. Furthermore, the heterogeneous nature of prairies, their continual display of form and color, and their representation at most levels of the moisture gradient, make these natural communities an invaluable addition to the landscaper's repertoire.

A FLORISTIC SURVEY OF INDIAN BOWL WET PRAIRIE.

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Indian Bowl wet prairie lies on the floodplain of the St. Joseph River in central Berrien County, Michigan. The area provides an excellent opportunity for study due to its large size (approximately 90 acres), its history of little disturbance, and the abundance of several species threatened in the state. Two series of quadrat samples were taken of the herbaceous vegetation of the wet prairie. The mid-July and end-of-August samples each encountered 37 taxa. In mid-July the prairie was co-dominated by *Carex* and

Solidago. Thelypteris palustris and *Filipendula rubra* were also important. The August sample indicated no dominant species for the wet prairie. The species with the highest relative dominance values were *Solidago* spp. (21.9), *Carex* (15.7) and *Sorghastrum nutans* (11.2). These 3 taxa comprise approximately 50% of the cover of the wet prairie. In both the July and August samples the Asteraceae were best represented, not only in dominance but also in numbers of taxa. The August sample included more species of the Poaceae than the mid-July sample. Of the 180 species of vascular plants collected from the wet prairie, 5 are on the Michigan threatened list: *Filipendula rubra, Silphium integrifolium, Trillium recurvatum, Polemonium reptans,* and *Cypripedium candidum. Filipendula rubra* is abundant in the prairie, while *Cypripedium candidum* is very rare. This area most closely fits the description of a wet prairie from a comparison of indicator species of fen, southern sedge meadow, wet, wet-mesic, and mesic prairie.

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PHOTODOCUMENTATION OF THE LOSS OF PRAIRIE WITHIN PERE MARQUETTE STATE PARK, JERSEY COUNTY, ILLINOIS. William E. McClain, Illinois Department of Conservation, Division of Forest Resources and Natural Heritage, Lincoln Towers, 524 S. 2nd Street, Springfield, Illinois 62706

Loess hill prairies are a prominent feature of the landscape within Pere Marquette State Park in Jersey County, Illinois. Examination of aerial photographs indicate that five of these prairies have been reduced in size by 150% from 1937 to 1974 due to woody plant invasion. Prescribed burning was introduced in 1973 to prevent further loss of prairie.

EVALUATION OF AN 8-YEAR-OLD PRAIRIE PLANTING ON AN INDUSTRIAL SITE IN WAUKESHA COUNTY, WISCONSIN. Darrel G. Morrison, Department of Landscape Architecture, University of Wisconsin, Madison, Wisconsin 53706

During spring 1974, a 32-ha planting of native grasses and forbs was installed at the site of the General Electric Medical Systems Division of Waukesha County, Wisconsin. The author designed the prairie planting, allocating different seed mixes to different portions of the site, based on topography and soils. The planting site included both abandoned farm fields and areas highly disturbed by the construction of extensive buildings, roads and parking areas.

Five different mixes of grass species were planted, using a Nesbit seed drill. Forbs were hand-broadcast in "islands" or aggregations, essentially superimposed over the drilled grass planting.

Except for clipping during the first (1974) growing season, the planting received almost no maintenance or management until April of 1980, when a controlled burn was conducted.

This extensive planting, with its small investment of management practices, is perhaps representative of others that might be implemented on other corporate or public sites. For that reason, an evaluation of its "success" may be of value to other landscape architects or corporations considering similar plantings.

The evaluation incorporated both a broad-scale visual assessment and quantitative sampling data. Aspects of the design and implementation which appear to have worked well were presented; modifications in technique that could lead to greater success in similar plantings in the future were also discussed.

APION ROSTRUM INFESTATION OF *BAPTISIA LEUCANTHA* SEED PODS: ITS POSITIVE EFFECT ON SEED GERMINATION RATE. Daniel C. Nepstad, Department of Botany and Plant Pathology, Michigan State University, E. Lansing, Michigan 48824

The larvae of *Apion rostrum* (Curculionidae) consume developing ovules of *Baptisia leucantha* (Fabaceae) while confined within its inflated seed pods. The *Apion* pupate and are contained within the pods until dehiscence. The pre-dehiscence seed crop of a *Baptisia* population in Kalamazoo County, Michigan, was harvested in April 1981. The total number of seeds (including partially eaten seeds) per pod was inversely proportional to the number of *Apion* per pod. Maximum number of fungus-infected seeds and maximum number of seed germinations per pod were found for pods with one *Apion*. Subsequent germination tests ($n = 100$; 4 replications) showed no significant differences in germination rates for fungus-infected, acid-scarified and mechanically scarified seeds (all ca. 6%), though all had significantly higher rates than intact, normal seeds and partially eaten seeds. A fungus is proposed as a seed-scarifying agent which is introduced into *Baptisia* pods by *Apion* and is responsible for the positive effect of seed-pod infestation on short-term germination of uneaten seeds.

A SURVEY OF THE NATIVE GRASSLANDS OF CASS COUNTY, MIGHIGAN. Robert J. Pleznac, Michiana Prairie Society, P.O. Box 667, Kalamazoo, Michigan 49005

Grasslands of the county are listed and described briefly. Methods used in discovering new sites are discussed as is the preservation and management potential of the various sites.

INFLUENCE OF MORTALITY ON SPECIES "DOMINANCE" AND DIVERSITY AMONG SEEDLINGS AND SHOOTS IN A TALLGRASS PRAIRIE. Jody K. Rapp and Deborah Rabinowitz, Division of Biological Sciences, University of Michigan, Ann Arbor, Michigan 48109

We followed the origins and fates of seedlings and vegetative shoots in artificial small disturbances and undisturbed controls from 1977 to 1980 in Tucker Prairie, Callaway County, Missouri. As mortality proceeds, the communities have lowered species richness, but "dominance" and equitability of the community of survivors remains unchanged from the pool of individuals which arose over the interval. This is to say, the dominance-diversity curves for survivors and for the pool of colonists are parallel, both for seedlings and vegetative shoots. Depletion of individuals does not alter the degree of "predominance" of one species "over" another.

But the survivors are not a random sample of the colonists. Some species have higher survivorship (for instance, 20% of the seedlings of *Panicum lanuginosum* over 4 years), and have some lower (8.5% of the seedlings of *Festuca paradoxa*). Despite this fact, a species' survivorship for seedlings is not related to its abundance in the source pool ($r_s = -0.57$, $n = 15$, $0.01 < P < 0.025$). Thus, we have no evidence that the mortality sieve is a competitive "sorting out" of successful from unsuccessful species.

PALEOETHNOBOTANY OF THE PRAIRIE REGION. Ann E. Sigford, Sigford & Johnson, Natural History Education and Design, Minneapolis, Minnesota 55407

A survey of recent paleoethnobotanical studies of prairie archaeological sites reveals surprisingly little evidence that wild prairie plants were gathered for food or utility. Most archaeological sites in prairie regions are found along rivers, and plant remains are typical of floodplains, forested slopes or disturbed ground. The most common class of archaeologically preserved wild plant food in prairie areas is nuts, including black walnut (*Juglans nigra*), hickory (*Carya* sp.), hazelnut (*Corylus* sp.) and acorn (*Quercus* sp.).

Prehistorically cultivated plants of tropical origin include squash, maize and beans. Native plants that were probably cultivated include sunflower (*Helianthus annuus*) and marsh elder (*Iva annua*). Other intensively harvested, but probably not cultivated, native plants include weedy members of the genera *Chenopodium, Amaranthus* and *Polygonum*. Some of these have been considered alien weeds, but their presence in archaeological sites thousands of years old suggests they are native.

Several factors may account for the absence of wild prairie plants in the archaeological record. Some of these include differential plant preservation, lack of excavated summer camps where prairie plants may have been collected, and unattractiveness of the prairie as a source of wild plant food. Prehistorically, the prairie may have been exploited more for its faunal resources, especially bison, than for its floral resources.

EFFECT OF ROUND-UP IN PRAIRIE RECONSTRUCTION.
Daryl D. Smith, Biology Department, University of Northern Iowa, Cedar Falls, Iowa 50614

The herbicide Round-up [N—phosphonomethyl glycine] was applied in May 1980 to a 7-year-old prairie reconstruction plot of 2 acres as a management tool in aiding establishment of native prairie grasses. Other plots were treated with more conventional management techniques, burning and mowing. Comparisons of treatments involved sampling, during the fall of 1980 and 1981, of prairie grasses and non-native species in terms of presence, frequency, % cover, biomass, and height.

UNIVERSITY OF NORTHERN IOWA BIOLOGICAL PRESERVES SYSTEM.
Daryl D. Smith, Biology Department, University of Northern Iowa, Cedar Falls, Iowa 50614

The UNI Preserves System is a complex of diverse natural lands and reconstruction areas, consisting of 5 tracts of land on campus encompassing 76 acres and 2 off-campus tracts of 78 acres. A tallgrass prairie reconstruction and a mixed-grass prairie reconstruction were initiated in 1973 and 1976, respectively. During summer 1982 an upland savanna reconstruction will be started. The preserves are intended to serve as outdoor laboratories as well as remnants of Iowa's natural heritage for future generations. The preserves also serve as demonstrations of management areas under a variety of uses.

PRAIRIES AS OUTDOOR LABORATORIES.
J. R. Holler, Department of Biology, University of Wisconsin-Platteville, Platteville, Wisconsin 53818.

Several different sample methods were employed by students to sample soil type, bacterial, animal and plant populations. Four different types of prairie situations were studied: mesic, xeric and 2 prairie restorations. Various sampling procedures were used including the line transect and quadrat methods. The Berlese funnel was employed for sampling of invertebrates. The dilution plate method was used for isolation of bacterial populations. Small rodent populations were examined by the use of snap traps and scat boards. Insect populations were determined by capture with nets.

ESTABLISHMENT OF FORBS IN GRASSLAND AREAS.
Jayne Traeger, Richard K. Sutton, and Sotero Salac, Department of Horticulture, University of Nebraska, Lincoln, Nebraska 68583

Many established grassland sites lack a full range of prairie forb species. These sites fall into 2 categories: (1) native prairies where forbs have become extinct due to mismanagement (overgrazing or extensive mowing), and (2) reseeded areas. Forbs may not be present in reseeded areas due to the unavailability of seed or failure in establishment. If present, forb species may be limited or inappropriate. Since forbs are important components of grassland ecosystems, a study was initiated to determine what culture practices are most successful in re-establishing forbs by direct seeding.

The study was initiated in the fall of 1981 at Twin Lakes, Seward County, Nebraska. The study site lies on a northeast slope within a tract of native prairie on clay loam soil. The establishment of 5 forb species, *Asclepias tuberosa*, *Petalostemum purpureum*, *Ratibida pinnata*, *Echinacea pallida*, and *Liatris punctata*, are currently being evaluated for 2 seeding dates (late fall and early spring) and 3 culture practices (mowing, burning, and herbicide plus mowing). Date and percent emergence, plant survival, rate of growth, and vigor of the forbs will be recorded for each treatment during the 1982 growing season.

SEED AND SEEDLING IDENTIFICATION OF PRAIRIE FORBS.
Jayne Traeger, Sotero Salac, and Richard K. Sutton, Department of Horticulture, University of Nebraska, Lincoln, Nebraska 68583

Photographic documentation of approximately 60 forb species has been initiated to provide an aid to amateur and professional prairie enthusiasts in seed collection and field identification. Seed and seedling stages for each species are included along with a botanical description, geographic range, and information on culture pertinent to each species. In addition, photographic and lighting techniques, and types of equipment used were discussed.

LICHENS IN THE NORTHERN GREAT PLAINS.
Thomas D. Trana, Department of Botany and Plant Pathology, Michigan State University, East Lansing, Michigan 48824

The lichen flora of the Great Plains of North America is poorly documented. Few collections exist from much of this area, and historical accounts are rare. Work has increased significantly in the last 20 years, but there are still few publications. A preliminary study of personal collections from North Dakota and adjacent portions of Montana and Minnesota indicates that whereas most species found in the northern Great Plains are widely distributed across North America, some species are more common in the Great Plains than elsewhere, and may truly represent a Great Plains floristic element. Some examples of such species are *Biatorella microhaema* Norman, *Candelariella subdeflexa* (Nyl.) Lettau, *Melanelia albertana* (Ahti) Essl., and *Physica melanchra* Hue, all of which grow on tree bark, and *Buellia elegans* Poelt, which grows on soil. Natural habitats for lichens in this region include glacial erratics, soil (especially in xeric grasslands), forests along creeks and in floodplains of rivers, aspen groves, and isolated cottonwood trees. Anthropogenic habitats such as fence posts, farmstead groves, and shingles on buildings may support species and assemblages of species different from those found on naturally occurring substrates. Of possible interest to grassland managers and ecologists are the results of a study to determine the affect of burning on the bryophyte and lichen vegetation of an oak savanna in central Minnesota. The Helen Allison Savanna has been under a controlled burning regime by The Nature Conservancy for the past 20 years. Most of the tract has been long unburned and serves as a control, while other portions have been regularly burned annually or at intervals of 1-3 years. In this study, led by C. M. Wetmore of the University of Minnesota and supported by The Nature Conservancy (Minnesota Chapter), we found that burning can decrease both species diversity and the amount of cover of those cryptogams growing on the soil and on tree trunks up to 1 m above the ground, even if the burning occurred only every fourth year. More frequent burning has an even greater affect. Thus in addition to decreasing biotic diversity, frequent burning will keep the soil between clumps of grass bare and allow greater soil erosion.

RESTORATION AND MANAGEMENT OF PRAIRIE TRANSITION COMMUNITIES IN CENTRAL MISSOURI.
J. Allen White, USDA Forest Service, Mark Twain National Forest, Cedar Creek Ranger District, Route 4, Box 67-A, Fulton, Missouri 65251

The purpose of this paper is to report on over 1,300 acres of prairie transition that have been restored and managed on the Cedar Creek Ranger District in Central Missouri since 1976. Over 5,000 acres of the district have been identified as originally being a tallgrass prairie, oak-hickory transition zone according to historical records and soil surveys. Existing vegetation includes exotic grass pastures, stands of off-site mixed oak and hickory, various stages of old-field succession and a few prairie transition remnants. The type of prairie transition restoration accomplished to date include re-establishment of mixtures of prairie grasses and forbs by conversion of existing pastures or old fields, restoration of existing remnant prairie transitions, and re-establishment of prairie transition, oak-hickory savannas from off-site wooded stands. Existing remnants appear to have the greatest short-term value as representative transition communities because of the natural diversity and spatial relationship to adjacent woodland savannas. However, because of the relative scarcity of remnants, re-establishments is the only alternative with potential for restoration of extensive prairie transition zones on Cedar Creek. Other than proper site selection, thorough site preparation and follow-up treatments are the most critical requirements of successful establishment and management. Interspersion of prairie and wooded types and maintenance of a wide ecotone are important facets of management on Cedar Creek. Future management direction should be to re-establish and manage at least 2,500 acres as prairie transition by 1985. The greatest obstacle seems to be uncertain funding..

AN EVALUATION OF DESIGN ELEMENTS OF A NATIVE PLANT COMMUNITY, THE SEDGE MEADOW.[1]

Pamela K. White, 1414 Tabor Ave., Apt. 214, Dayton, Ohio 45420

This paper reports exploratory research dealing with the seasonal change in design elements and design relationships within varied scenes of a wetland plant community. The research objectives were to apply the interpretive results to landscape design and restoration of native plant communities and to suggest future studies and approaches needed for design of restorations. Slides and plant species lists were systematically collected throughout the spring, summer, and fall seasons of 1980. Slide scenes were evaluated by descriptive graphic and written methods. This evaluation revealed interpretive results that have implications for the design and evaluation of the visual success of native community design, re-creation, and restoration.

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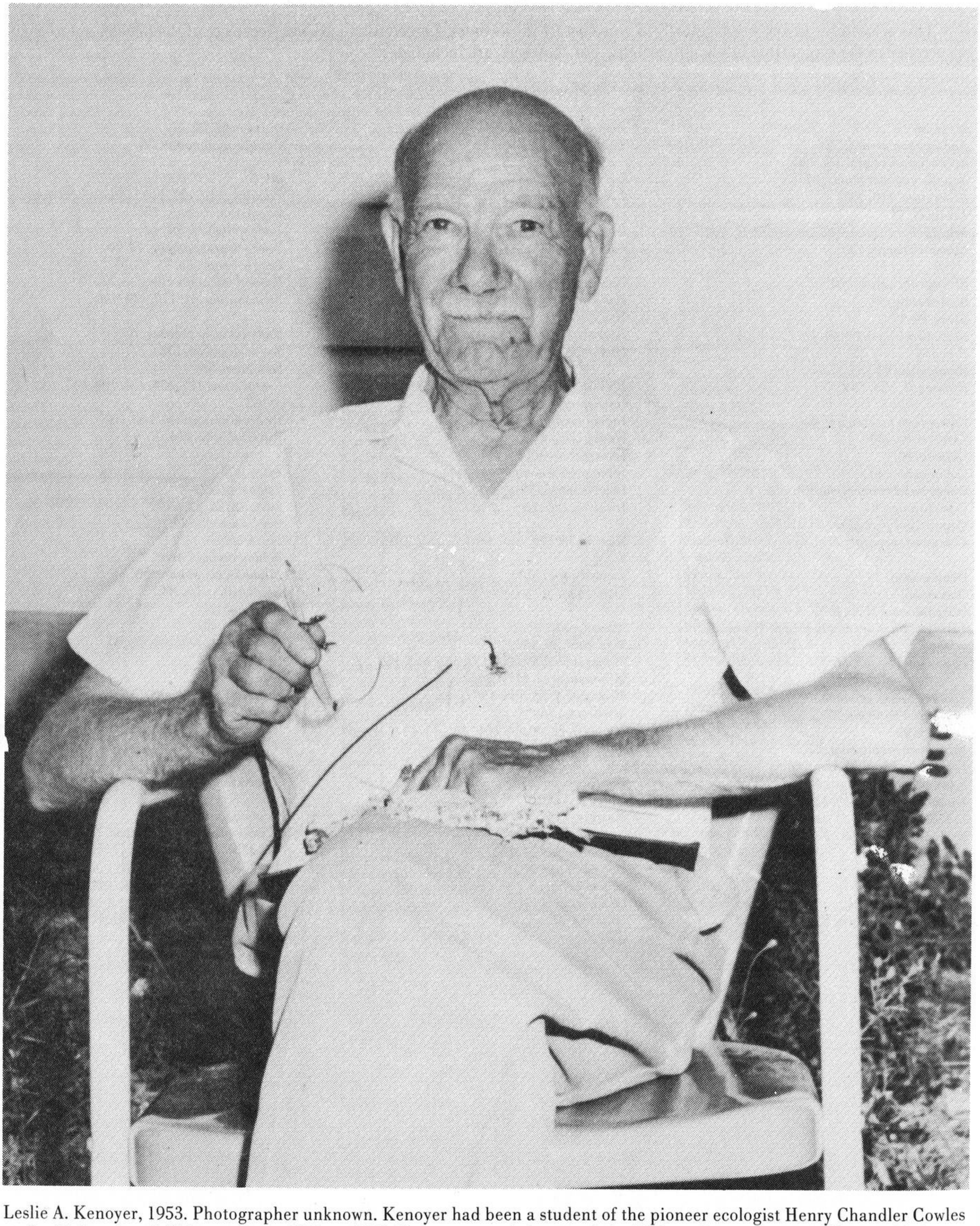
[1] White, P. K. 1982. Techniques for successful designing with native plants. NatureScape (January 1982): 15-18.

Author Index

Subject Index

This is an index to key words, mostly as supplied by the authors. The citation is to the first page of the article, not to each occurrence of the topic. Only full-length articles, not abstracts, are included.



Leslie A. Kenoyer, 1953. Photographer unknown. Kenoyer had been a student of the pioneer ecologist Henry Chandler Cowles at the University of Chicago. From 1923 to 1953 Kenoyer was chairman of the Biology Department at Western Michigan University. His series of papers making use of data from the early surveys dividing the region into Sections, Townships, and Ranges (such as *Forest Distribution in Southwest Michigan as Interpreted from the Original Land Survey*. Papers of the Michigan Academy of Science, Arts and Letters 19:107-111, 1934) are important sources of information about the mesic prairies of the state.

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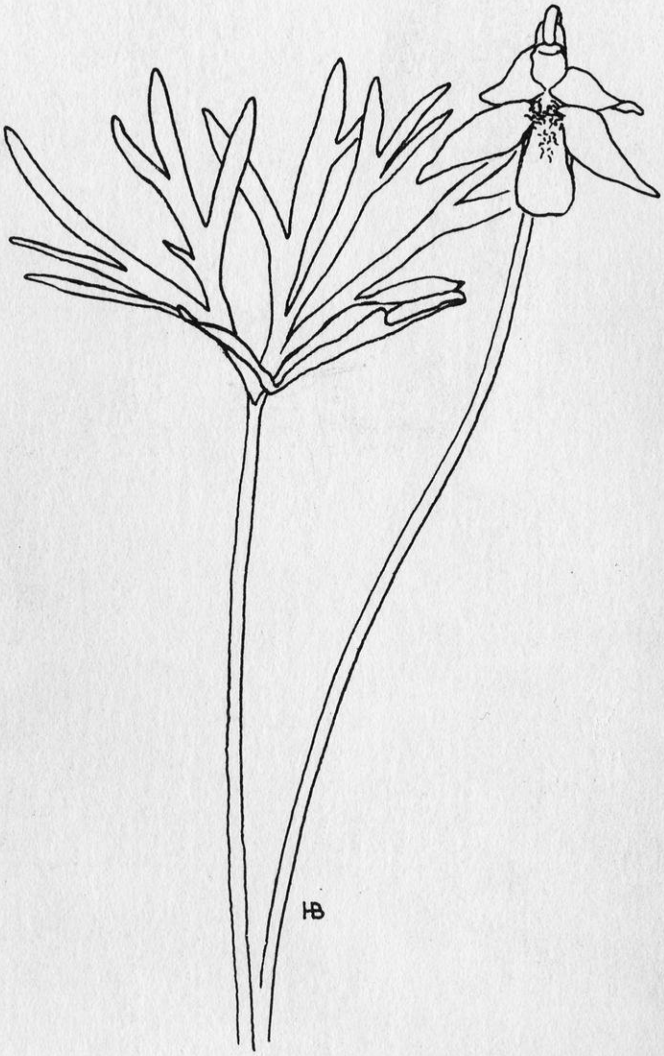

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