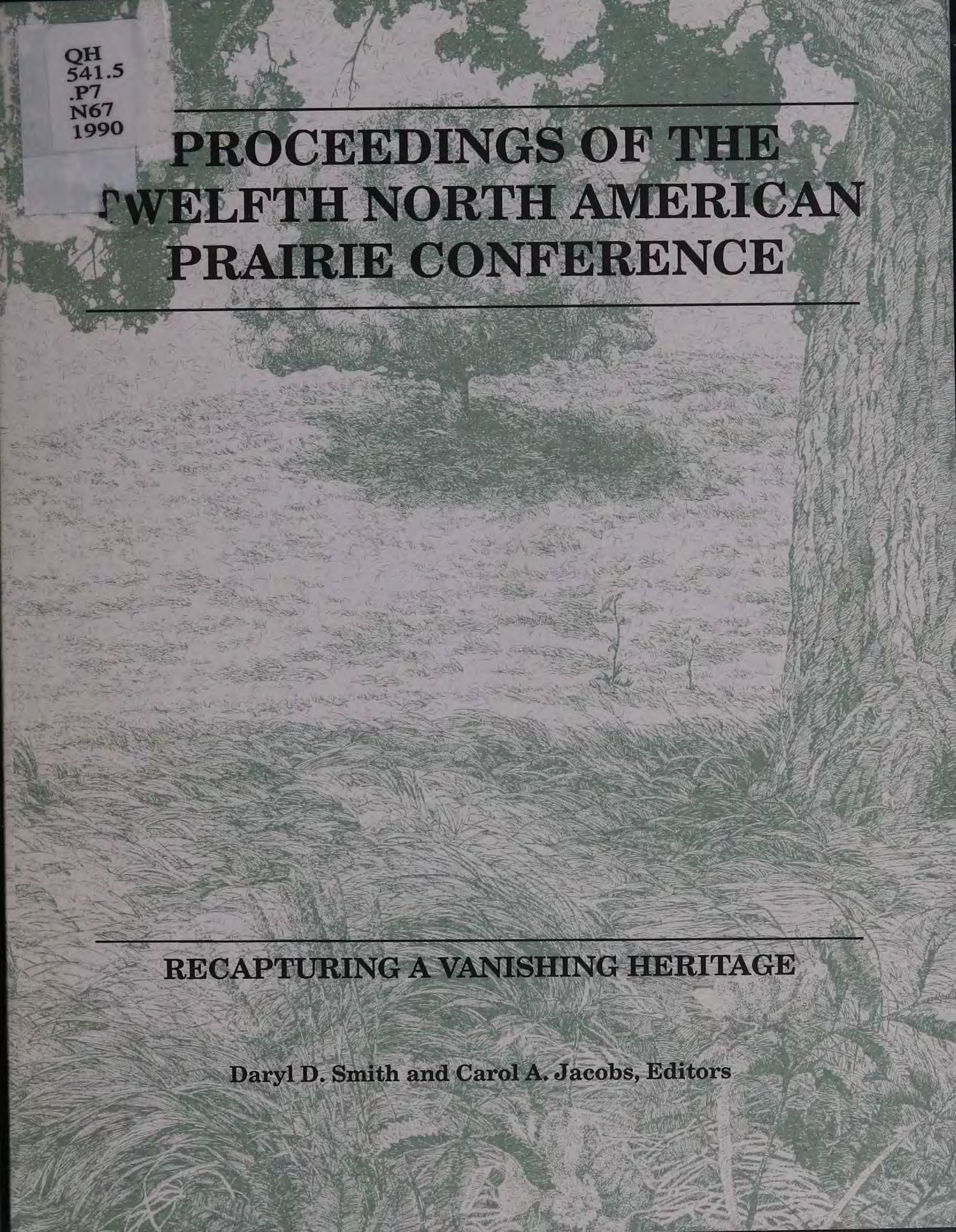


PROCEEDINGS OF THE TWELFTH NORTH AMERICAN PRAIRIE CONFERENCE

RECAPTURING A VANISHING HERITAGE

Daryl D. Smith and Carol A. Jacobs, Editors

NORTH AMERICAN PRAIRIE CONFERENCES

The Twelfth North American Prairie Conference was the most recent of a series of biennial meetings begun in 1968. Through the Fifth Conference, these meetings were referred to as Midwest Prairie Conferences. Reflecting the broadening interest in native grassland and savanna, later meetings have been termed North American Prairie Conferences.

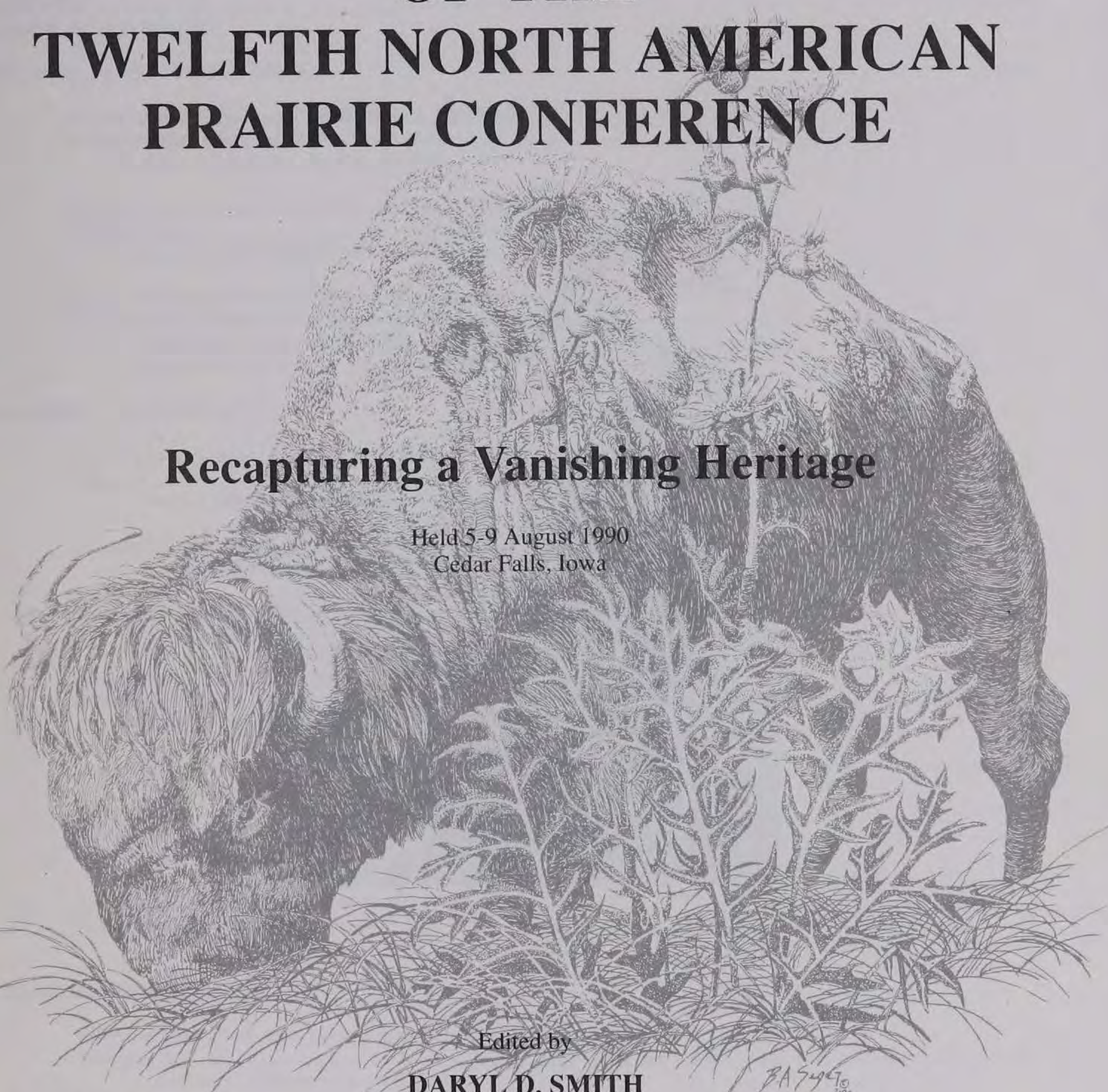
The previous Conference Chairs constitute the only "organization" for the Prairie Conferences. This group, or as many of the group as possible, meets at some time during each Conference to determine the host for the next North American Prairie Conference. Other than this, there is neither a central organization nor a budget. Coordination between the present and previous Conference Chairs has proved adequate to organize each meeting; local financial assistance has been used to meet required expenses.

Listed below are the chairs, locations, and dates of the twelve prairie conferences to date. In addition, on the inside back cover a listing of all conferences is given in the suggested citation format. Additional information, including how to order copies, is included in brackets.

NORTH AMERICAN PRAIRIE CONFERENCES 1st-12th:
CHAIRS, LOCATIONS, AND DATES

1st. Peter Schramm, Knox College, Galesburg, Illinois. 14-15 September 1968
2nd. James H. Zimmerman, University of Wisconsin, Madison. 18-20 September 1970
3rd. Lloyd C. Hulbert, Kansas State University, Manhattan. 22-23 September 1972
4th. Mohan K. Wali, University of North Dakota, Fargo. 19-21 August 1974
5th. David C. Glenn-Lewin and Roger Q. Landers, Iowa State University, Ames. 22-24 August 1976
6th. Ralph E. Ramey, Ohio State University, Columbus. 12-17 August 1978
7th. Clair L. Kucera, Southwest Missouri State University, Springfield. 4-6 August 1980
8th. Richard Brewer, Western Michigan University, Kalamazoo. 1-4 August 1982
9th. Richard H. Pemble, Tri-College University Center for Environmental Studies, Moorhead, Minnesota. 29 July-1 August 1984
10th. Arnold Davis, Geoffrey Stanford, and Madge Lindsay, Texas Woman's University, Denton. 22-26 June 1986
11th. Thomas B. Bragg and James Stubbendieck, University of Nebraska, Lincoln. 7-11 August 1988
12th. Daryl D. Smith, University of Northern Iowa, Cedar Falls. 5-9 August 1990

PROCEEDINGS OF THE TWELFTH NORTH AMERICAN PRAIRIE CONFERENCE



Recapturing a Vanishing Heritage

Held 5-9 August 1990
Cedar Falls, Iowa

Edited by

DARYL D. SMITH

and

CAROL A. JACOBS

Printed on Recycled Paper

University of Northern Iowa, Cedar Falls

Cover illustration and special artwork throughout were created for the Proceedings by Brian A. Seger of Cedar Falls, Iowa.

Proceedings of the Twelfth North American Prairie Conference: Recapturing a Vanishing Heritage.

Printed in the United States of America.

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PRAIRIE: MANAGEMENT

ROADSIDE PRAIRIE: STUDIES AND PROGRAMS

PRAIRIE: RESTORATION AND RECONSTRUCTION

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- Pioneer Hi-Bred International
- Participants of Twelfth North American Prairie Conference
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  - -Biology Department
  - -College of Natural Sciences
  - -Continuing Education
  - -Integrated Roadside Vegetation Management: County Assistance Office

PREFACE

What a thousand acres of Silphiums looked like when they tickled the bellies of the buffalo is a question never again to be answered, and perhaps not even asked.
Aldo Leopold, 1949
A Sand County Almanac

The midcontinent prairies of North America must have been an awesome sight to those viewing them for the first time. Mile after mile of grasses and forbs reaching to the horizon would have been overwhelming. The limitless nature of the landscape created a feeling of insignificance similar to that inspired by the ocean; "sea of grass," an expression often used by the early prairie travelers, evokes the vastness of the prairie ecosystem. This vastness created an illusion for the early settler that the prairie could never be subdued. However, increasing masses of settlers with improving technological tools of cultivation did conquer the prairies. Today only small patches of the original prairie remain, islands scattered across an agricultural sea. Most of the prairies were gone before there was recognition of what was being lost. By the turn of the nineteenth century most Iowa prairies had been converted to agricultural use, but very few noted their passing or bemoaned their loss; it was 1933 before consideration was given to preserving Iowa prairies. Aldo Leopold's quote cuts to the heart of the matter. We have lost so much of the prairies that it is difficult to visualize what they were once. And, as a society, we often appear not to be concerned about their loss. The biennial North American Prairie Conferences provide opportunities to attempt to answer Leopold's question and to gather momentum in beginning to ask it. "Recapturing a Vanishing Heritage," the theme for the Twelfth North American Prairie Conference, accurately portrays the efforts of participants in attempting to understand, preserve, reconstruct, restore, manage, and interpret remnants of the midcontinent prairies. In one way or another, amateur naturalists, poets, land managers, biologists, geographers, historians, artists, and many more are involved in recapturing some facet of our prairie heritage. As in previous conferences, people with a variety of backgrounds and interests gathered to exchange ideas and help recapture our vanishing prairie heritage.

The Twelfth North American Prairie Conference was held in the heart of the tallgrass prairie region. Prior to settlement 85% of the Iowa landscape was prairie. The deep, black-soil prairie which covered most of the state now constitutes a significant portion of the prime agricultural land of North America. In addition to the black-soil prairie, presettlement Iowa contained sand prairies, hill-prairie openings, prairie sloughs, fens, oak savannas, rock-outcrop prairies, and the internationally unique Loess Hills. From 5 to 9 August 1990, 527 prairie proponents from 20 states and 3 Canadian provinces gathered on the campus of the University of Northern Iowa, Cedar Falls, Iowa to exchange experiences and ideas about North American prairies.

Institutions that contributed financial or service support for the conference and the proceedings are acknowledged on page *vi*. The success of the conference was enhanced by the contributions of field trip leaders, section chairs, and discussion leaders:

Bill Blankenship
Diane Blankenship
Peter Breussler
Pauline Drobney
Bohdan Dziadyk
Alan Ehley
Larry Eilers

Kathy McKee
Jay Norton
Mary Norton
Steven Packard
John Pearson
Ethan Perkins
Gary Phillips

Donald Farrar
Bernard Hermanson
George Hoffman
Kay Kleir
Mark Leoschke
Jean Prior
Dean Roosa
Sue Smith
James Walters
Arnold Webster

The contributions of Nancy Osborne and the Continuing Education Center were invaluable.

Conference participants presented 99 papers, including 8 invited papers and 10 poster papers. In addition to the regular sessions on basic ecology, restoration and reconstruction, management, fire ecology, and prairie culture, special symposia were held on roadside prairie studies and programs, savannas, and environmental education for the prairie. An award was presented to Peter Schramm in appreciation of his foresight in initiating the first Midwest Prairie Conference in 1968. Roger Landers, Director of the Fifth Midwest Prairie Conference, was given an award in appreciation of his contributions to prairie preservation, activism, and research in Iowa. A program and abstract booklet was provided for all conference registrants. A limited number of these booklets are still available at a cost of $2.00 postpaid for handling and shipping (make check payable to the University of Northern Iowa and mail to Daryl Smith, Department of Biology, University of Northern Iowa, Cedar Falls, Iowa 50614-0421.)

The Proceedings of the Twelfth North American Prairie Conference includes 47 of the papers from the conference. Each manuscript was reviewed by at least one person in addition to the editorial staff. Reviewers are listed on page *vii*. Their careful reviews, constructive criticisms, and prompt responses are much appreciated. We also thank the authors for their cooperation in providing prompt, responsive revisions, even when such revisions required significant modification of the original manuscript. We especially acknowledge Dorothy Grant, Sandra Hendrickson, Joy Miller, Jennifer Gronewold, and Kelly Goldsmith for their efforts in reviewing, processing, or coordinating manuscripts and graphics preparation.

Daryl D. Smith
Carol A. Jacobs
6 April 1992

GRASSLAND ECOSYSTEMS AND CLIMATE CHANGE: HYPOTHESES FOR THE NORTHERN GRASSLAND-BOREAL FOREST ECOTONE

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Abstract. Global circulation models simulating a doubling of the atmospheric CO_2 concentration suggest that warming will be sufficient to cause grassland ecosystems to expand northward over the next 30-50 years. These models predict a northern expansion of grasslands and parklands from 14% to 35% of the land area in western Canada. Climate changes would occur more rapidly than in the past. There is good correlation between the present distribution of existing grassland remnants in the boreal forest and those parts of the forest expected to acquire a grassland climate. Species will respond individually to the effects of CO_2 fertilization and climatic parameters. Ecotones between grasslands and other biomes will be fruitful research sites for measuring the earliest impact of climate change. Research at the northern grassland-boreal forest ecotone in Alberta, Canada, has shown that, with fire suppression, aspen forest has expanded at the expense of grasslands in recent decades. Fire is expected to increase in both frequency and intensity in a greenhouse climate and could play a pivotal role in reducing the cover of forest. Examples are described in which special circumstances of fire and land use practices remove the regeneration niche of tree species and result in greater cover of grasses.

INTRODUCTION

There is general agreement among scientists that the rising concentrations of CO_2 and other greenhouse grasses will lead to dramatically higher temperatures over most of the earth's surface in the next few decades. There is mounting evidence that the earth is now experiencing a warming trend (Bolin et al. 1986); several of the warmest years on record have occurred in the last decade. It is uncertain whether the present warming can be linked to the greenhouse effect in a cause and effect relationship.

General circulation models (GCM) of the earth's atmosphere have been used to project climatic parameters after a doubling of CO_2. Such projections suggest an increase in the global mean surface temperature of 1.5-4.5C. Simulations of preindustrial climate suggest a post industrial increase of 0.3-1.1 C, in agreement with the observed rise in global mean temperatures (0.3-0.7C) over the past 100 years (Bolin et al. 1986). The predictions of global warming over the next 50 years have spectacular implications for vegetation and the distribution of biomes. Temperature change following glaciation is thought to be of the same magnitude (Bolin et al. 1986). Deglaciation resulted in large scale migrations (several thousand kilometres) of plants in thousands of years.

A central theme of plant biogeography is that biomes and, consequently, characteristic plant types are linked to climatic parameters in integrative and predictable ways. For example, climatically determined grasslands occur on parts of the globe where soil moisture is lower than that required for forests, yet sufficient for the growth and maintenance of grasses. Such areas occur in the rain shadow of mountain ranges or are situated between forests and deserts (Lauenroth 1979).

Holdridge (1967) developed a scheme to describe the distribution of vegetation based on the assumption that vegetation type is largely determined by the interaction of temperature and rainfall. Holdridge's model fits the observed vegetation pattern reasonably well, and his scheme is simple enough to use as a predictive tool for vegetation patterns if the GCM temperature and precipitation predictions are correct. Emanuel et al. (1985a) used this approach, with refinements (Emanuel et al. 1985b, Rowntree 1985), to generate the global distribution of vegetation after a doubling of CO_2.

The revised simulations of Emanuel et al. (1985b) show a tremendous areal expansion of grassland climate at the expense of forests in western Canada (for map see endpapers of Bolin et al. 1986). For western Canada only, south of the arctic circle, we quantified this as an increase of 21%. The implication is that, given time for soil development and species replacement, grasslands or parklands would become the potential vegetation of much of the southern boreal forest in western Canada.

In this paper, we discuss the distribution of prairie remnants in the boreal forest and possible mechanisms for conversion of forest to grassland under climate change. We suggest that fire will play a pivotal role. Under climate change some species will increase in abundance and range, while others will decrease.

METHODS

We examined northern grassland remnants from central Alberta (55°N) to the Alberta-Northwest Territories border (60°N) and in the Yukon Territory. We made notes of the general character of each site visited, collected plant specimens, and examined the soils. More detailed descriptions of some of these sites are published elsewhere (Moss 1952, Redmann and Schwarz 1986, Schwarz et al. 1988). Sites we were unable to visit include two sites in the Northwest Territories for which there are published descriptions (Raup 1947, Thieret 1959). Other sites in the Northwest Territories and Manitoba are known to us through herbarium records of species usually thought to be associated with the grassland region. Both sites in Saskatchewan are known to us through other ecologists (R. Johnson and R.T. Coupland, personal communications).

DISCUSSION

Distribution

The central grasslands of the United States may change in character, but according to the simulations of Emanuel et al. (1985a, b), they will not undergo much change in regional distribution. By contrast, the grasslands of Canada are expected to expand northward to include areas of Alberta, Saskatchewan, and the District of Mackenzie, Northwest Territories, that are presently forested. In addition, isolated pockets of grassland climate are expected to expand in Alaska and the Yukon Territory (Emanuel et al. 1985b, for map see endpapers of Bolin et al. 1986).

Grassland remnants within the boreal forest have a high concentration of species that are considered grassland species in terms of origin and present distribution (Redmann and Schwarz 1986, Schwarz et al. 1988). Examples are porcupine grass [*Stipa curtiseta* (A.S. Hitchc.) Barkworth], green needle grass (*S. viridula* Trin.), spear grass (*S. comata* Trin. & Rupr.), Hooker's oat grass [*Helictotrichon hookeri* (Scribn.) Henr.], plains blue grass (*Poa arida* Vasey), mat muhly [*Muhlenbergia richardsonis* (Trin.) Rydb., a C_4 species], brittle prickly pear [*Opuntia fragilis* (Nutt.) Haw., a CAM species], long-fruited anemone (*Anemone cylindrica* A. Gray), three-flowered avens (*Geum triflorum* Pursh), and graceful cinquefoil (*Potentilla gracilis* Dougl. *ex* Hook).

Grassland remnants have a low cover of shrubs and are treeless. The canopy of adjacent forest is nearly always aspen (*Populus tremuloides* Michx.). Grassland remnants occur on steep (25-70%) slopes with an east to southwest aspect, occasionally on west facing slopes, but never on north slopes. On level sites, these grasslands are associated with exceptionally good drainage, such as on high river bluffs or on thin soils underlain by bedrock or sites with moderate soil salinity at depth (Wilkinson and Johnson 1983, Redmann and Schwarz 1986). The soil texture is usually clay, but steeper slopes may be lighter textured. The soil profile appears characteristic of grassland rather than forest soils (Redmann and Schwarz 1986).

With few exceptions, these grassland remnants are found within those areas expected to acquire a grassland climate as a consequence of doubling the CO_2 concentration (Figure 1). These remnants may have originated when the climate was warmer and grassland extended farther northward, or they may simply be a reflection of the modern climate that in this region tends to be drier than other parts of the boreal forest. Regardless of origin, the distribution of these remnants suggests that with climate warming there is indeed potential for grassland expansion in this part of the boreal forest.

Species Response

The effects of elevated CO_2 varies among plant species (Kimball 1983, Cure 1985), suggesting that changes in competitive balance among species may occur. The exact physiological reasons for differences in the CO_2 response among C_3 plants are unclear. Consequently, the second order, or ecological level, of response is even more difficult to project. Nevertheless, it seems likely that new associations of plants will develop in response to new climatic regimes, as well as to the direct effects of CO_2. The direct effects of CO_2 could act quite independently of climate to produce unexpected changes in the distribution and competitive ability of species. Little is known about how CO_2 fertilization will affect the competitive relationships of native species and what changes will occur in natural ecosystems.

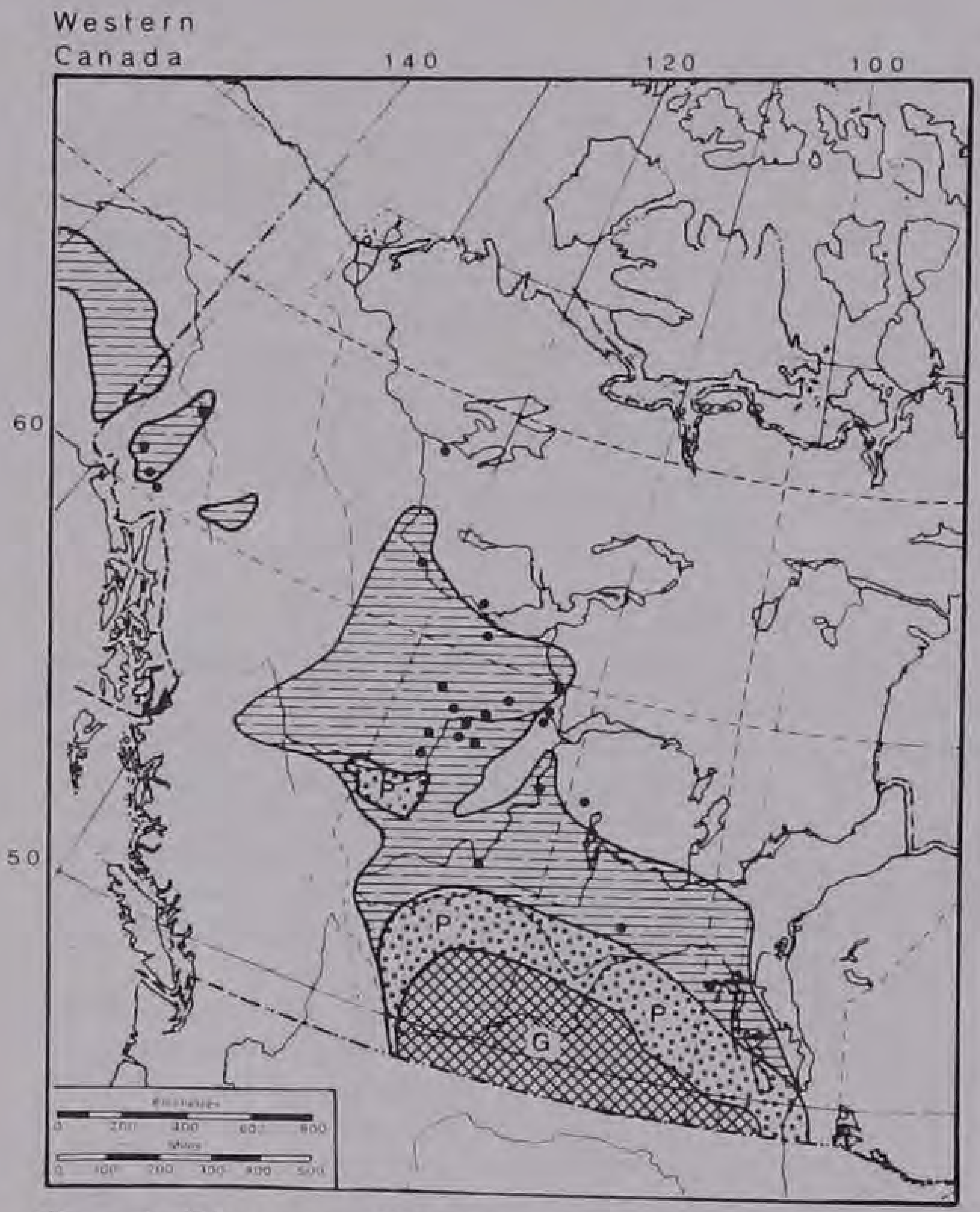

Figure 1. The present distribution of grasslands (G, cross-hatching) and aspen parklands (P, open-dot pattern) in western Canada. The areas with horizontal lines are those areas expected to acquire a grassland climate as a consequence of doubling of CO_2 (redrawn from endpaper map in Bolin et al. (1986)). The solid dots indicate the occurrence of disjunct prairie remnants within the present boreal forest.

Based on limited comparisons, Cure (1985) has noted that CO_2 fertilization appears to be more effective among broad-leaved plants than among grasses. We can hypothesize that aspen may be a successful species in the "greenhouse environment". Expansion of aspen forests bordering grasslands is now occurring and may continue in coming decades.

Ecotones

Long term study of ecotone dynamics should prove to be useful in resolving the fate of grasslands and forests in northern Alberta. Studies in this region could provide the earliest indication of vegetation change that might be linked to the greenhouse effect.

Aspen parkland, a climatically influenced regional ecotone 50-200 km wide, is a major transition zone between the forest and grassland biomes. The aspen parkland has been described as a climatic tension zone (Bird 1961) in that the ecotone vegetation types invade one another in response to climate changes. At the regional scale, observation by remote sensing could be used to document vegetation change through time.

By contrast, local ecotones, which are transitional between communities, a few meters wide, may be understood to be a consequence of soils, topography, drainage, fire history, or land use patterns. The influence of these local factors is unlikely to be expressed equally throughout the regional ecotone. Local ecotones are amendable to experimental manipulation, as well as repeated observation. Experiments using prescribed fire or transplant gardens, for example, could provide climate change analogues along edaphic or topographic gradients.

Disturbance Processes

It is difficult to imagine how grassland might replace established forest without some sort of natural or economically motivated disturbance. Wildfire, insect attack, disease outbreaks, or agricultural and forestry operations all provide mechanisms for removal of the tree canopy and result in a situation where tree and grass propagules compete. Under the present climate and disturbance regimes, grasses dominate at an early stage of succession, but this is usually temporary, and the forest is re-established in a few years. However, under a new climate and disturbance regime, the regeneration niche of the forest species may be lost.

In the time since settlement, prairie fires have been eliminated or reduced, and aspen appears to have migrated southward on a regional scale (Bird 1961). There is anthropological evidence that, for a variety of reasons, native groups in the boreal forest used fire to create and maintain openings in the forest (Lewis 1982, Lewis and Ferguson 1988). Almost certainly, some prairie remnants in the boreal forest owe their existence to fires of this origin. Others may exist for edaphic or topographic reasons as noted above. Under the present levels of enhanced fire suppression, grassland remnants are being lost to invasion by aspen. On one grassland remnant near 59° N latitude, the aspen forest edge advanced 10-50m over 37 years (1945-1982). Most of this vegetation change was evident by 1955 (Schwarz et al. 1988).

Fire has always played an important role in the boreal forest, and decades of fire suppression may have led to a fuel buildup in aspen forests, such as those surrounding grassland remnants. Under the warmer, drier climatic conditions proposed for coming decades, wildfire may be expected to increase in both frequency and intensity (Ryan 1989, Wein 1990, Flannigan and Van Wagner 1991). Fire suppression systems are technically sophisticated and increasingly effective in suppressing most fires, especially those under low hazard conditions. However, the ecologically significant fires (large scale and intense) will still occur and resist control because agencies responsible for fire suppression have limited resources. The current trend of forest invasion of grasslands may be reversed in coming decades.

Potential Mechanisms for Conversion of Forest to Grassland

One scenario for conversion of jackpine (*Pinus banksiana* Lamb.) forest to grassland is repeated fire. Jackpine requires fire for regeneration. After a single fire, jackpine seedlings establish and grow quickly with a cover of herbs and grasses. Among these species is hairy wild rye (*Elymus innovatus* Beal), a ubiquitous species of dry and mesic boreal forest sites. Hairy wild rye occurs widely in the understory of jackpine and increases cover dramatically after fire. Jackpine growing in dense stands with hairy wild rye may produce enough fuel to carry a second fire within a few years. If the second fire occurs before jackpine seedlings have begun to produce cones (ca. 6-10 years), trees would be eliminated (Keays 1987). The site would remain in grass until trees colonize through long distance seed transport.

The greatest economic use of the boreal forest is the harvest of lumber and fibre for the pulp and paper industry. At present, these industries are entering a period of expansion into areas that have potential grassland climates under the "greenhouse environment" scenario. One of the difficulties with regeneration of white spruce [*Picea glauca* (Moench) Voss] after harvest is interference by blue-joint [*Calamagrostis canadensis* (Michx.) Beauv.]. Occasionally, a heavy sward of blue-joint shades spruce seedlings and changes the soil thermal regime (Hogg and Lieffers 1991), effectively removing the regeneration niche of white spruce. The oldest of these grass-dominated communities have persisted for many years with no prospect of quickly returning to productive forest.

Prescribed fire and grazing have been shown to be effective range management tools to convert mature aspen forest to productive rangeland (Fitzgerald and Bailey 1984, Bailey et al. 1990). Fire was used to kill aspen stems, and a single heavy late grazing reduced aspen to 2.5% of available forage. Continued grazing prevented re-establishment of a forest canopy.

Wildfire and heavy bison use in the Lake One-Square Lake region of Wood Buffalo National Park have apparently contributed to the demise of groves of aspen and balsam poplar (*Populus balsamifera* L.). Such areas are distinguished by a vegetative cover of grasses and forbs, an absence of immature trees, and burned stumps in growth position.

Conclusions

The view that vegetation change due to the greenhouse effect will involve northward expansion of parklands and grasslands is widely held. The existence of grassland remnants in those parts of the boreal forest expected to acquire a grassland climate lends credence to this scenario. These grassland remnants, with species compositions similar to the parklands several hundred kilometres to the south, could provide propagule sources for the spread of grasslands.

In recent decades, the areal extent that many grassland remnants have lost to aspen invasion is thought to be a consequence of fire suppression. The possibility exists that aspen may experience more enhanced growth than other plants in a high CO_2 environment, but research is required to confirm this.

Regardless of aspen response to CO_2, fire and land use will play an important role in the conversion of forest to grassland. Wildfire is expected to increase as a result of climate change, even with sophisticated fire management systems. Grazing and forest harvesting are increasing and may contribute to removal of the regeneration niche of forest species, creating a grassy environment. A new climatic regime may maintain the grassy vegetation type.

The mechanisms by which grasslands might establish on sites formerly occupied by forest are poorly understood. There is a need for experiments directed at climate change hypotheses, involving both the species and ecosystem levels. Ecotones should provide important sites for permanent plots. Remote sensing could be used to monitor large regions over time. The prospect of climate change challenges scientists and managers alike to engage in long-term research and planning for the future.

ACKNOWLEDGEMENTS

This study was part of a project funded by the Natural Science and Engineering Research Council of Canada (Research Assistantship in forestry to A.G.S. and Operating Grant to R.W.W.) and a Boreal Alberta Research Grant (A.G.S.). We are grateful for the cooperation of the management and staff of Wood Buffalo National Park. We thank J.C. Hogenbirk, E.H. Hogg, and R.A. Wright for thoughtful discussion.

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NITROGEN CYCLING, PLANT COMPETITION, AND THE STABILITY OF TALLGRASS PRAIRIE

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Abstract. Five perennial grass species (*Schizachyrium scoparium* (Michx.) Nash, *Andropogon gerardi* Vitman., *Poa pratensis* L., *Agropyron repens* (L.) Beauv., and *Agrostis scabra* Willd.) were grown on an experimental soil nitrogen (N) gradient. In competition plots on low-N soils, the two prairie bunchgrasses, *Andropogon* and *Schizachyrium*, completely displaced the other three species within three years. However, displacement did not occur on high-N soils. In N-cycling studies using monocultures, the two prairie species reduced soil N supply rates compared to the other species by tying up N in their slowly decomposing litter. These species, therefore, create the low-N conditions for which they are superior competitors. This positive feedback between plant competition and N cycling may be a critical process in tallgrass prairie. Alteration of the N cycle can disrupt this feedback, however. High rates of atmospheric N deposition caused by air pollution may be sufficient in parts of the Midwest to seriously threaten the stability of tallgrass prairie remnants.

INTRODUCTION

Prior to settlement, the tallgrass prairie covered a vast section of North America. Considering the dramatic variation in soil type and climate within this region, the vegetation was surprisingly uniform. The dominant plant species were a set of warm-season grasses: big bluestem (*Andropogon gerardi* Vitman.), little bluestem (*Schizachyrium scoparium* (Michx.) Nash), Indian grass (*Sorghastrum nutans* (L.) Nash), and switchgrass (*Panicum virgatum* L.). How the tallgrass prairie was able to dominate such a large and diverse region and why, on the other hand, it was so vulnerable to numerous disturbances, including overgrazing and the invasion of exotic species, is only beginning to be understood. In the last few decades, ecologists have recognized the critical role of fire in maintaining tallgrass prairie (Knapp and Seastedt 1986, Axelrod 1985). The results presented in this paper suggest nitrogen (N) cycling may also play a critical role.

Experiments, both in the Kansas Flint Hills (Owensby et al. 1970, Seastedt et al. 1991) and in Minnesota sand prairies (Tilman 1987), have shown that N is the nutrient most frequently limiting the productivity of tallgrass prairie in non-drought years. Thus, the widely held assumption that moisture limitation is the primary constraint on productivity in tallgrass prairie (Weaver 1954) needs to be reconsidered. In contrast to increased productivity due to N addition, water addition did not result in significant increases in productivity (Owensby et al. 1970, Tilman 1990). Using several different precipitation parameters as predictors, only 14% of the variability in above-ground net primary production could be accounted for in a 50 year study of tallgrass prairie in the Kansas Flint Hills (Towne and Owensby 1984). This contrasts sharply with the strong correlation of precipitation and productivity found in the short- and mixed-grass prairies of the Great Plains (Sala et al. 1988). Nutrient dynamics, especially for N, must be addressed in understanding the structure and functioning of the tallgrass prairie ecosystem. In this paper, we review and summarize the previously published results of experimental studies comparing the N dynamics of prairie and non-prairie grasses, discuss the unique N cycle of the tallgrass prairie, and suggest that disruption of the N cycle may be important in the destabilization of tallgrass prairie.

METHODS

This research was part of the Long Term Ecological Research program at the University of Minnesota's Cedar Creek Natural History Area. Cedar Creek is located on a glacial outwash sandplain in east-central Minnesota. These studies focused on the five most abundant grasses in the abandoned old fields and native prairies at Cedar Creek. Little bluestem and big bluestem are native warm-season bunchgrasses dominant in late-successional fields and undisturbed prairies and oak savannahs. Ticklegrass (*Agrostis scabra* Willd.) is a native, cool-season bunchgrass found in early successional fields. Quackgrass (*Agropyron repens* (L.) Beauv.) and Kentucky bluegrass (*Poa pratensis* L.) are both non-native, cool-season rhizomatous grasses found in early- to mid-successional fields at Cedar Creek (Tilman 1988). These species were planted as monocultures and in mixed-species plots on soils ranging from sand (0.3% organic matter and 90 mg of N per kg of dry soil) to a sandy-loam black soil (3.0% organic matter and 1,100 mg/kg total N). By mixing different ratios of these two soils, an experimental gradient in soil fertility from low N to high N conditions was created. Black-soil plots that received an additional 5.6 g N m^{-2} yr^{-1} as NH_4NO_3 fertilizer were the most fertile plots of the gradient. To insure that N was the only soil resource limiting growth, all plots were watered and fertilized with all nutrients except N. The controlled garden situation allowed us to address 1) the N-use efficiency of these grasses (Wedin 1990), 2) their competitive interactions under high- and low-N conditions (Tilman and Wedin 1991a, Wedin 1990), and 3) their effects on N cycling (Wedin and Tilman 1990) and soil NH_4 and NO_3 concentrations (Tilman and Wedin 1991b). These various experiments are only summarized here; complete methods and results can be found in the above citations.

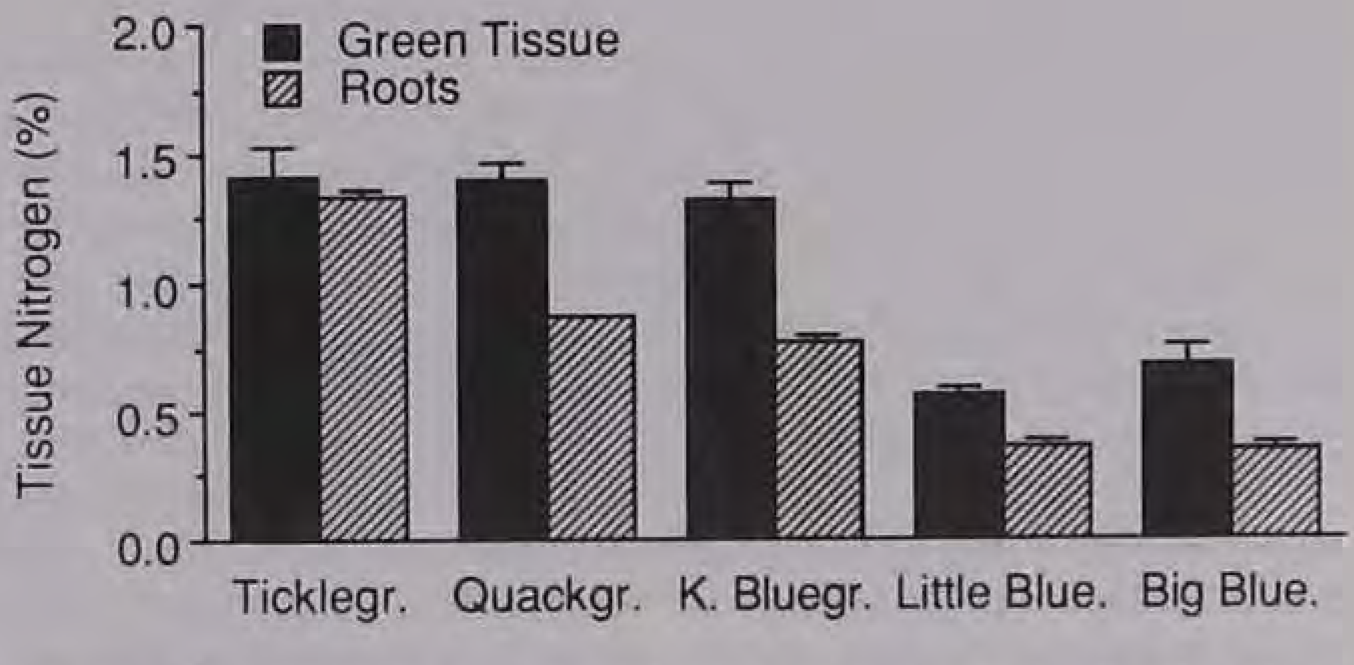

Figure 1. Tissue N concentrations (means and standard errors) in late July for five grass species (ticklegrass, quackgrass, Kentucky bluegrass, little bluestem and big bluestem) growing in monocultures on a sandy-loam black soil.

RESULTS AND DISCUSSION

Nitrogen-Use Efficiency

Little and big bluestem had low tissue N concentrations in both their leaves and roots compared to the cool-season grasses (Figure 1). The same pattern is seen in the N concentration of dead tissues, although values are somewhat lower following senescence for all species (Wedin and Tilman 1990). These low N concentrations are not simply due to differences among the species in photosynthetic pathway, that is, C_4 (warm season) versus C_3 (cool season). The warm-season grasses which dominate the moisture-limited Great Plains (blue grama and buffalo grass) have tissue N concentrations considerably higher than the 0.5%-0.7% found in mid-season green tissues of big and little bluestem in the N-limited tallgrass prairie. Thus, the two prairie grasses have high N-use efficiency, that is, they produce a unit of biomass with a very low investment of N (Chapin 1980, Vitousek 1982).

The two bluestems also allocated a large proportion of their biomass below ground, a pattern well documented by Weaver (1958) and others. In the three-year-old monocultures growing on black soil, 70% of the annual net productivity of big and little bluestem occurred below ground, while 52% occurred below ground for quackgrass and Kentucky bluegrass, and only 15% for ticklegrass (Wedin 1990). After three years, the below-ground biomass of the two bluestems (approximately 1200 g/m^2 for both species) was over twice that of either quackgrass or Kentucky bluegrass (approximately 500 g/m^2) and over twenty times that of ticklegrass (45 g/m^2)(Wedin 1990, Tilman and Wedin 1991b). Thus, these two prairie grasses have a high N-use efficiency and, because of their large root system, are efficient at acquiring below-ground resources, including N.

Interspecific Competition

Little bluestem and big bluestem completely displaced the other three grasses within three years in the mixed-species plots on the infertile, sandy soils (Tilman and Wedin 1991a, Wedin 1990). In pairwise competition experiments with little bluestem versus quackgrass or Kentucky bluegrass, little bluestem completely eliminated the two non-native species on the low-N soils even when little bluestem was added as seed to one-year-old monocultures of the competing species. However, at the high end of the fertility gradient, little bluestem did not have a competitive advantage over quackgrass or Kentucky bluegrass (Wedin 1990).

The competitive advantage of the two prairie species on the infertile soils corresponded to their ability to deplete the concentration of available soil N to lower levels than the three other species. The concentration of available soil N, estimated as 0.01M KCl-extractable soil NO_3 and NH_4, was significantly lower in the three-year-old little bluestem and big bluestem monocultures than in the monocultures of ticklegrass, quackgrass, and Kentucky bluegrass (Tilman and Wedin 1991b). These differences among monocultures in the concentration of available soil N were highly correlated with differences among the species in root biomass (Tilman and Wedin 1991b). However, at the high end of the fertility gradient, the two prairie species did not deplete available soil N to levels significantly lower than did Kentucky bluegrass and quackgrass. This corresponded to the lack of a competitive advantage for big and little bluestem over the two non-native, cool-season species under more productive conditions.

These competition results are consistent with other Cedar Creek experiments. When N was added (as NH_4NO_3 fertilizer) to a sand prairie at Cedar Creek dominated by little bluestem, high N addition rates (greater than 9 g N m^{-2} yr^{-1}) led to the complete displacement of little bluestem by Kentucky bluegrass and quackgrass after seven years (Tilman 1987, 1990). A shift in species composition and the loss of dominance by little bluestem occurred at N addition rates of only 1 to 2 g N m^{-2} yr^{-1} (Tilman 1990). Although originally present in smaller amounts than little bluestem, big bluestem showed the same decline following N addition (Tilman 1987).

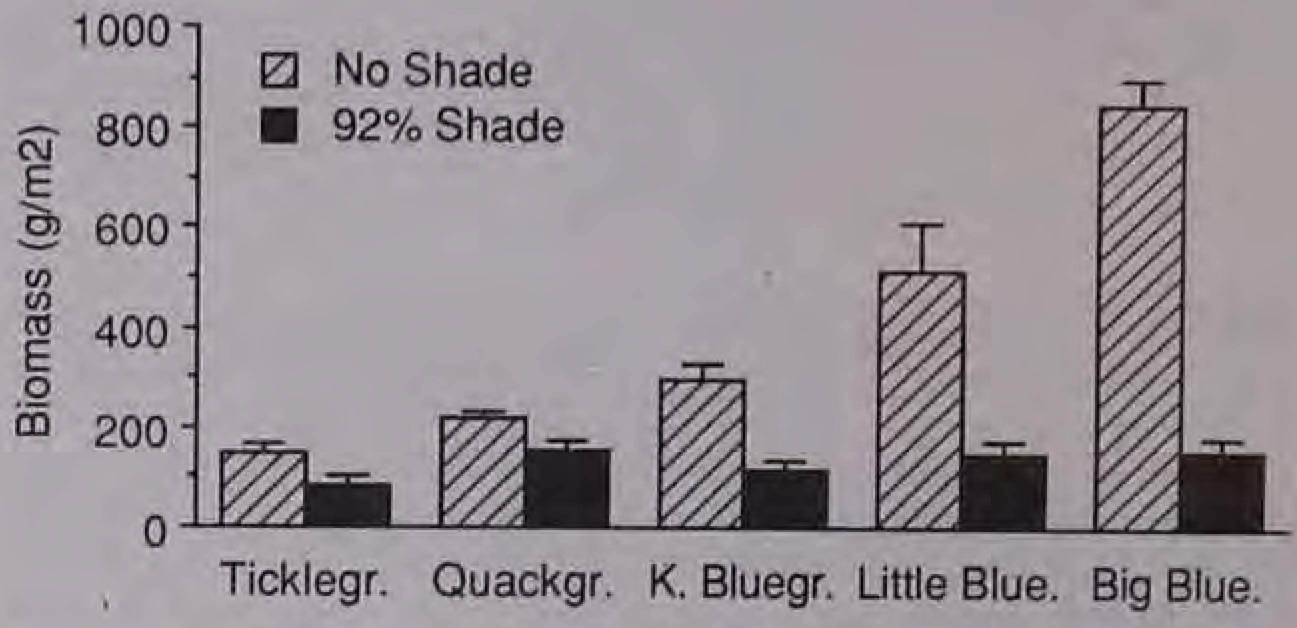

Figure 2. Effects of shade (92% of ambient light removed) on the total (above- and below-ground) biomass of three-year-old monocultures of five grass species growing on a mixed (sand and sandy-loam) soil (means and standard errors).

Why do the two prairie grasses lose their competitive advantage when N supply rates and productivity increase? A consequence of high N-use efficiency and high allocation of biomass to roots is vulnerability to light limitation, which becomes more important with increasing productivity (Chapin 1980, Knapp and Seastedt 1986, Tilman 1988). In a related study, monocultures of these five grasses were grown under different levels of shade. Under heavy shade, the two bluestems had a much larger drop in biomass than the other three grasses, most of which was caused by a dramatic drop in root biomass (Figure 2). The two bluestems also had large increases in their tissue N concentration under heavy shade, an increase of approximately 200% compared to an increase of approximately 50% for the three cool-season species (Wedin 1990). Thus, the traits which appear to confer a high competitive ability for N to the two prairie grasses are severely impacted by light limitation. We conclude, therefore, that the competitive superiority of the warm-season prairie grasses disappears with the shift from a N-limited to a light-limited environment.

Decomposition and Nitrogen Cycling

The supply rate of N in most terrestrial ecosystems is determined largely by the rate of N mineralization, the rate at which NH_4 and NO_3 are released from decomposing organic matter in the soil. Because the decomposition rate of litter (dead plant material) can vary depending on the quality of that litter, differences in litter quality among plant species can lead to differences in N cycling (Vitousek 1982). Litter types with low N concentrations and high lignin concentrations provide a low quality substrate for the decomposers. The litter of big and little bluestem has a very low N concentration and has been shown to decompose very slowly, tying up, or immobilizing, available N for more than two years, before it begins to release, or mineralize, N (Pastor et al. 1987a, Seastedt 1988).

We used an *in situ* incubation technique to measure the N mineralization rates in the five species' monocultures over three years (Wedin and Tilman 1990). By the third year of the study, there was a dramatic divergence in N mineralization rates under the different species, with low rates (1-2 g N m^{-2} yr^{-1}) in the big and little bluestem plots, intermediate rates (3-4 g N m^{-2} yr^{-1}) in the quackgrass and kentucky bluegrass plots, and high rates (12 g N m^{-2} yr^{-1}) in the ticklegrass plots at the black soil end of the experimental fertility gradient. These differences in N mineralization rate were highly correlated with the differences among the species in the quantity and quality of litter produced, especially below ground

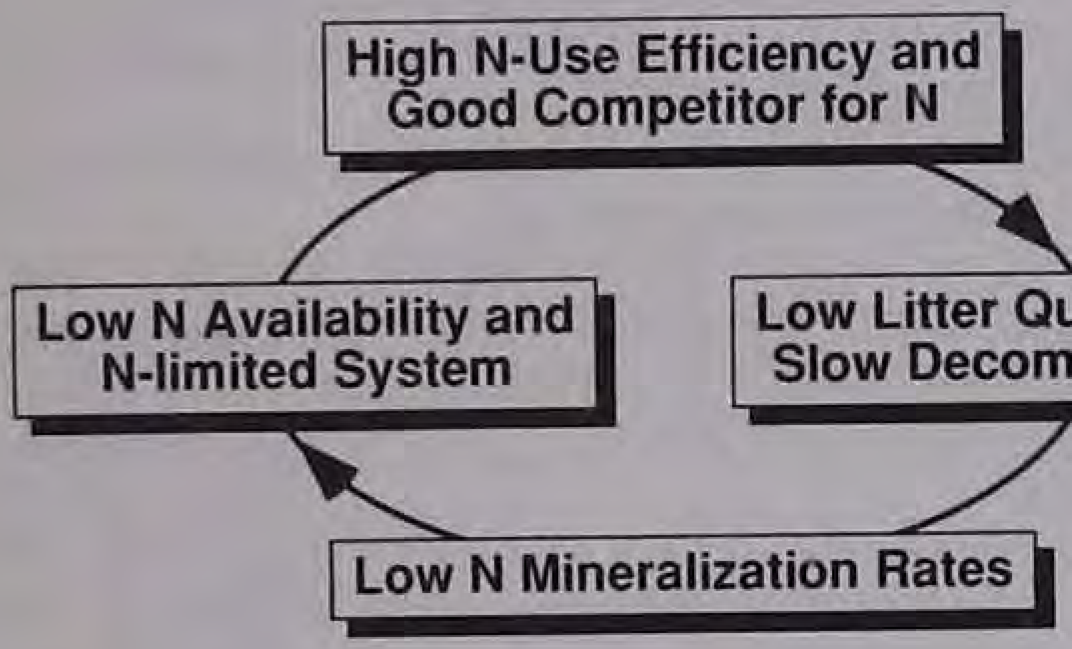

Figure 3. A proposed positive feedback between plant competition and N cycling for the tallgrass prairie.

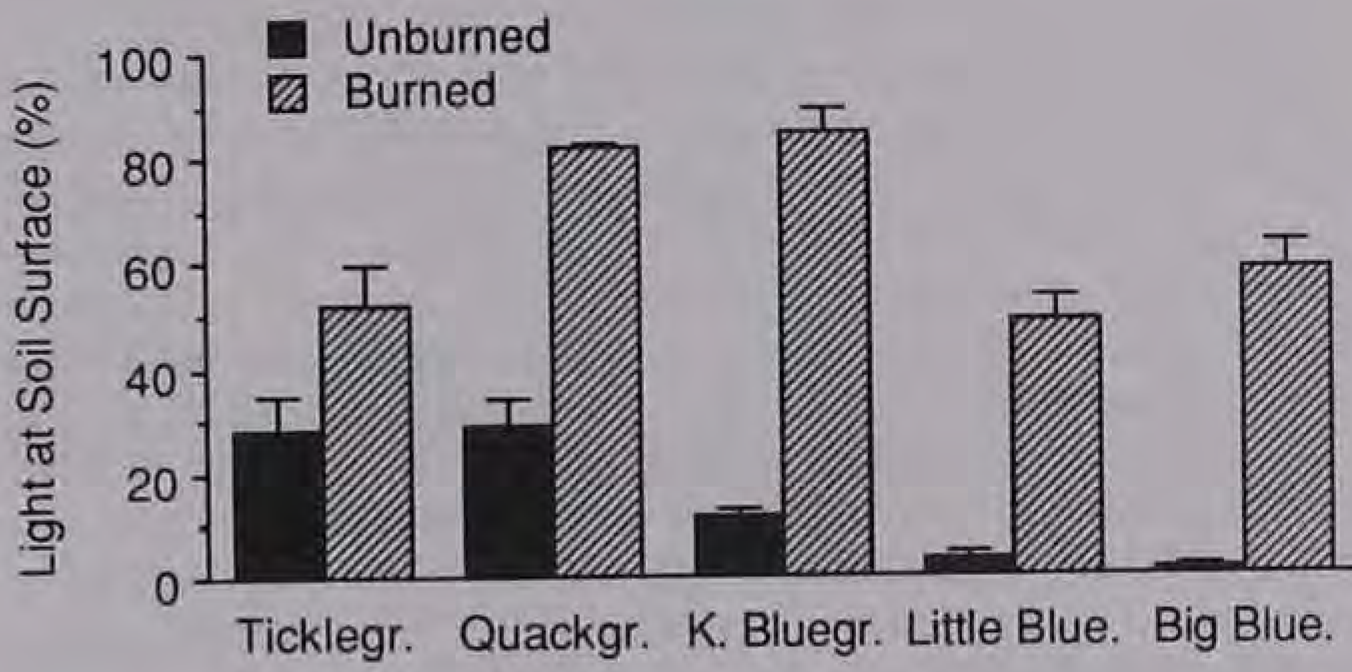

Figure 4. Light penetration (means and standard errors) in unburned monocultures with five years' litter accumulation and burned monocultures of five grass species on a sandy-loam black soil.

(Wedin and Tilman 1990). Sharp reductions in N mineralization rates in plots of big and little bluestem corresponded to their production of large amounts of low N organic matter below ground.

Nitrogen Cycling and the Stability of Tallgrass Prairie

Summarizing the results of these various experiments: the warm-season prairie grasses are able to produce biomass with low investments of N, that is, they have a high N-use efficiency, and they allocate most of their biomass below ground. Because of this, they are able to deplete the amount of available soil N to low levels, making them good competitors under N-limited conditions. Finally, their low litter quality leads to slower N cycling and a reduction in the soil's N supply rate. Together, these factors create a positive feedback: through their effects on N cycling, these warm-season grasses create a N-limited environment in which they have a competitive advantage (Figure 3). Part of the reason tallgrass prairie was able to dominate such a large and diverse area may be that the dominant prairie grasses created a favorable N cycle over a wide range of climates and soils.

A characteristic of positive feedback systems, however, is that they are vulnerable to disruption (DeAngelis et al. 1989). Given a large enough disturbance, they are inherently unstable. This may partly explain why the tallgrass prairie was vulnerable to so many types of disturbance. Disruption of the feedback at any point can lead to the system's collapse and its replacement by another system, such as a Kentucky bluegrass or quackgrass field. An important disruption of this positive feedback in the tallgrass prairie is litter accumulation caused by lack of fire. The low litter quality of little bluestem and big bluestem that results in reduced N supply rates also leads to slow decomposition and the accumulation of above-ground litter. After five years, the unburned monocultures of the two prairie grasses had accumulated more above-ground litter than the other three species, even though all species had comparable above-ground productivities on the sandy-loam black soil. Consequently, light penetration (the percent of available light at the soil surface) in the unburned monocultures of big and little bluestem was almost zero (Figure 4). In comparable burned monocultures, however, there was no litter accumulation and light penetration was relatively high for all five species. As discussed above, under light-limited conditions the competitive advantage of the warm-season prairie grasses declines. Fire is critical, therefore, because it prevents heavy litter accumulation under the prairie grasses and thus prevents a shift from N limitation to light limitation (Knapp and Seastedt 1986). The faster the rate of litter accumulation, that is, the more productive the prairie, the more critical fire becomes.

Other disturbances which can disrupt the positive feedback between the warm-season prairie grasses' competitive ability and their effects on N cycling include overgrazing, soil disturbance, and climate changes. Heavy grazing leads to decreased N-use efficiency and decreased below-ground biomass allocation, both of which affect the prairie grasses' ability to compete for N and their feedback effects on N cycling (Holland and Detling 1990). Grazers also return, via urine, a high proportion of the N they consume, increasing the N supply rate (McNaughton et al. 1988). Soil disturbance or shifts in climate will also affect decomposition and N mineralization rates. Fertilizing a tallgrass prairie with N is a direct disruption of the prairie N cycle and leads to an increase in nonnative grasses and forbs (Owensby et al. 1970, Tilman 1987).

A more subtle, but potentially important, disturbance to the tallgrass prairie is the dramatic increase in rates of atmospheric N deposition in the last 30 years caused by increased levels of both NO_3 and NH_4 in air pollution. Emissions of NO_3 are primarily caused by the burning of fossil fuels and are highest in the industrial eastern Midwest. Emissions of NH_4 come from the use of NH_4 fertilizer and from intensive livestock operations and are higher in the western part of the Midwest. Both fossil fuel consumption and N fertilizer use have increased sharply since World War II. For example, N fertilizer use nationwide quadrupled between 1960 and 1980 (National Research Council 1989).

In 1989, N deposition in precipitation ranged from roughly 0.4 g N m^{-2} yr^{-1} on the western edge of the tallgrass prairie in eastern Kansas and Nebraska to over 0.8 g N m^{-2} yr^{-1} in southern Michigan (National Atmospheric Deposition Program / National Trends Network 1990). The actual N deposition rates experienced by prairie remnants in the Midwest may be considerably higher than this for two reasons. First, although measurements of N deposition in dryfall (gas exchange and fine particulates) are quite inaccurate, data from NADP/NTN and the NOAA/ATDD CORE/Satellite network (Meyers and Sisterson 1989) suggest that the wetfall data can be increased by a factor of 1.5 to approximate total N deposition in the Midwest. Total atmospheric N deposition estimates therefore range from roughly 0.6 g N m^{-2} yr^{-1} on the western edge of the tallgrass prairie to over 1.2 g N m^{-2} yr^{-1} in the eastern Midwest. Given a N mineralization rate in tallgrass prairie soils of 3-6 g N m^{-2} yr^{-1} (Risser and Parton 1982, Pastor et al. 1987b, Ojima et al. 1990), atmospheric deposition has increased N supply rates on the order of 10-25%. A second consideration is that NADP/NTN sites are chosen to be away from local sources of air pollution, such as urban centers, fertilized fields, or feedlots. Many prairie preserves are in just such areas. Some of these preserves probably have N deposition rates greater than 2 g N m^{-2} yr^{-1}, N addition rates which led to the displacement of little bluestem by Kentucky bluegrass and quackgrass in Cedar Creek experiments (Tilman 1987, 1990).

There has been a chronic loading of N to prairie remnants in the Midwest over the last 20-30 years. The resulting increases in productivity may lead to the loss of tallgrass prairie species and the invasion of exotic grasses and woody vegetation. The invasion of cool-season rhizomatous grasses, such as quackgrass, Kentucky bluegrass, and smooth brome, in prairie remnants in the eastern Midwest is a widespread management problem, particularly in sites surrounded by agricultural fields. Increased N deposition from both regional and local sources may be one cause of this problem. Clearly, further research is needed to understand the role of this disturbance. One implication, however, is that managers may need to rethink their fire regimes. The natural fire regimes that are thought to have occurred in pre-settlement times may be less relevant under modern conditions of higher productivity and faster litter accumulation. More frequent fires would not only prevent increased litter accumulation, but would also volatilize most of the N in litter (Ojima et al. 1990), helping to counteract N loading from atmospheric deposition. Of course, managers must also consider the impact of increased fire frequency on forbs, invertebrates, and other prairie components.

In conclusion, the N cycle is a critical component in our understanding of the tallgrass prairie ecosystem. We suggest that the disruption of the distinctive N cycle found in the tallgrass prairie is a significant threat to the prairie. In contrast to overt disturbances of the prairie, such as tilling, overgrazing, fertilization, or the exclusion of fire, recent increases in atmospheric N deposition rates are a subtle threat that merits further consideration, particularly in the eastern Midwest.

ACKNOWLEDGEMENTS

We thank the researchers, staff, and summer workers at Cedar Creek for their advice and assistance throughout the course of this research, especially N. Johnson, J. Pastor, P. Woutat, J. Rozinka, and D. Disch. Carol Simmons from NADP/NTN (Fort Collins) provided data and advice on atmospheric deposition. The research was supported by the National Science Foundation, the Dayton/Wilkie Fund of the University of Minnesota, and Prairie Restorations Inc.

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EFFECTS OF TALLGRASS PRAIRIE VEGETATION ON THE CONCENTRATION AND SEASONALITY OF NITRATE-NITROGEN IN SOIL WATER AND STREAMS

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Abstract. Inorganic nitrogen concentrations in tallgrass prairie soils and streams exhibit a sinusoidal seasonal pattern; nitrate levels are relatively high in winter and low in summer. The pattern is not observed in either rainfall or canopy drip (throughfall). Thus, the pattern is created by plant root-microbial interactions; when roots are not active, nitrates accumulate and can be leached from the soil. We used nitrogen fertilizer and herbicide in a factorial experiment to test the strength of root uptake activities on soil water nitrogen. Soil-water nitrate concentrations were 10 times higher when prairie roots were deactivated by application of a foliar herbicide. Ammonium nitrogen concentrations were unaffected. When fertilizer was added, nitrate levels of soil water beneath herbicide-treated vegetation were double that of untreated prairie. Mineralization of nitrogen from herbicide-treated roots was not believed to be the source of the increased nitrate. These and previous studies at Konza Prairie emphasize the importance of plant cover in maintaining low nitrate concentrations of streams.

INTRODUCTION

The progressive enrichment of groundwaters and streams with nitrate-nitrogen from agro-ecosystems, feedlots, and urban areas is a serious and intensifying problem in the Midwest. While much of this nitrogen has been imported into the area in fertilizers, the disturbed prairie soils also contribute a vast amount of inorganic nitrogen to streams. In contrast, undisturbed prairie soils lose only a fraction of the nitrogen entering the soil to groundwater and streams (Hayes and Seastedt 1989). Nitrogen conservation is brought about by a complex set of interactions among plant roots, soil microbes, and the physical and chemical properties of prairie soils. Plant roots function in the short term to actively remove nitrogen from the soil and in the long term to provide the source of fixed carbon that ultimately binds soil nitrogen into highly stable organic matter. Here, we present data showing the extent to which the prairie vegetation and soils modify the concentrations of nitrate-nitrogen, and we evaluate the influence of root uptake of nitrogen on the seasonal patterns observed for soil and streamwater nitrate-nitrogen.

METHODS

Research was conducted on the Konza Prairie Research Natural Area in the Flint Hills of northeastern Kansas, a site owned by The Nature Conservancy and managed by Kansas State University. Vegetation of this tallgrass prairie has been described by Gibson (1989). Konza Prairie is a Long-Term Ecological Research (LTER) site and has been involved in a study of plant and soil nitrogen dynamics for almost a decade. The nitrate chemistry of rainwater has been measured routinely as part of the National Atmospheric Deposition Program (NADP). In this study, weekly nitrate concentrations as measured by NADP were averaged by month for the 1982-1988 period. The composition of precipitation reaching the soils differs markedly from that measured above the vegetation canopy (Seastedt 1985). This liquid, termed canopy drip or throughfall, collected in a series of throughfall troughs, has also been measured on a weekly or rainfall event basis since 1982 (Seastedt 1985, Gilliam 1987). Nitrate concentrations of throughfall were averaged by month for the 1982-1989 period. Similar measurements of soil-water nitrates were obtained at 20 cm depths of soil using porous cup lysimeters (Hayes and Seastedt 1989). Soil water can be obtained using this method only when the soil is at or near field capacity. Also, samples cannot be obtained under freezing conditions; hence, measurements were limited to the spring and early summer (March-early July) interval.

Konza Prairie receives about 83 cm of rainfall per year, and about 75% of the precipitation occurs in the growing season, April-September (Bark 1987). May and June are the two wettest months. This pattern of rainfall produces a strong seasonal component in both soil moisture and streamflow (Tate 1990). In general, streams tend to become dry midway through the growing season and do not begin to flow consistently again until the soils have been recharged by autumn, winter, or early spring rains. Baseflow in streams is supported by groundwater emerging at springs (seeps) found at limestone-shale interfaces (Tate 1990). In the present study, four springs were sampled for nitrate every other week during 1984. While streamflow in spring and early summer is fairly predictable, flow during other periods of the year is very unpredictable and related to specific storm events. Stream water samples have been taken at weekly intervals (provided the streams were flowing) since 1986. Only samples taken during non-storm (baseflow) periods were included. Also, only nitrate concentrations for the first seven months of the year are reported here, because samples obtained later in the year reflect specific storm events rather than groundwater-supplied baseflow. Additional details regarding the complexity of the stream environment are reported in Tate (1990).

An experiment to measure the influence of plant roots on soil water ammonium and nitrate-nitrogen concentrations was conducted during the growing season in 1987 on a single site divided into 24 small plots. In each 4 m x 4 m plot, a porous cup lysimeter was installed to sample soil water at 20 cm depth. Lysimeters were installed in early spring, approximately six weeks prior to the initiation of the experiment. A three-factor factorial design was used to test for the effects of living or dead plant roots, nitrogen additions, and fixed carbon (sugar) additions. In early June, a foliage-applied herbicide (Roundup) was used to kill vegetation surrounding 12 of the lysimeters. Within the herbicide and no herbicide treatments, six plots were fertilized with nitrogen and six plots were fertilized with carbon. Nitrogen was applied as granular ammonium nitrate at the rate of 10 g N.m-2. Carbon plots were treated biweekly with three equal applications of table sugar to total 100 g C.m-2 applied to a 0.25 m2 area centered on the lysimeter. This additional carbon source stimulates microbial activity which in turn removes inorganic nitrogen from the soil (Seastedt et al. 1988). Three replicates of each of the eight possible combinations of treatments were created. Plots were watered to assure adequate penetration of the nitrogen and carbon into the soil. Soil water was collected for all plots one month after herbicide and nutrient additions. In spite of this, several of the lysimeters failed to produce sufficient water samples for analysis.

Analytical procedures for measuring nitrogen concentrations in the various types of water samples have been described elsewhere (Seastedt 1985, Hayes and Seastedt 1989, Tate 1990). Nitrate concentrations (reported as µg NO3—N.l-1) were not converted to nitrogen amounts; hence, reported values have not been weighted by sample volume. Values reported are means and standard errors for variable but extensive data sets. Except for seep measurements, the shortest descriptive data set reported here was three years in length and included both wet and dry years. Hence, we believe that the results present a range of climatic conditions typical of the tallgrass prairie ecosystem. The statistical analysis of the experimental study used transformed data (ranks) instead of actual numbers in order to homogenize treatment variances.

RESULTS

Nitrate concentrations in rainwater lack any consistent seasonal pattern except, perhaps, for a late winter peak (Figure 1). By the time rainwater has been leached through the vegetation canopy, a strong bimodal pattern in concentrations is observed (Figure 2). The canopy can add chemicals to and remove chemicals from rainwater; these chemicals move to or from the air (dryfall impaction) and the vegetation itself. Microbes and invertebrate herbivores on the vegetation also influence the chemical composition. We do not know the exact mechanism(s) causing the observed pattern in throughfall nitrate concentrations, except to state that the February peak is generated by abiotic activities, probably originating outside of Konza Prairie. The second peak appears to be a biological phenomenon related to on-site characteristics.

Soil-water, springs, and stream-baseflow nitrates are 1) much lower in nitrogen concentrations than either rainfall or throughfall and 2) exhibit a pattern opposite that of throughfall (Figures 3, 4, and 5). Values are significantly larger in winter or early spring and decline to levels almost two orders of magnitude lower than those observed above ground. These concentrations are sufficiently low to inhibit or at least greatly reduce the amount of algae growing in Konza Prairie streams (Tate 1990). Both the soil-water and the spring results suggest that concentrations of nitrates increase prior to the senescence of vegetation in late summer. This pattern may be the result of nitrates being concentrated in a reduced water volume or the result of short-term storm events. The results might also suggest, however, a reduction in plant root uptake of nitrogen during this interval.

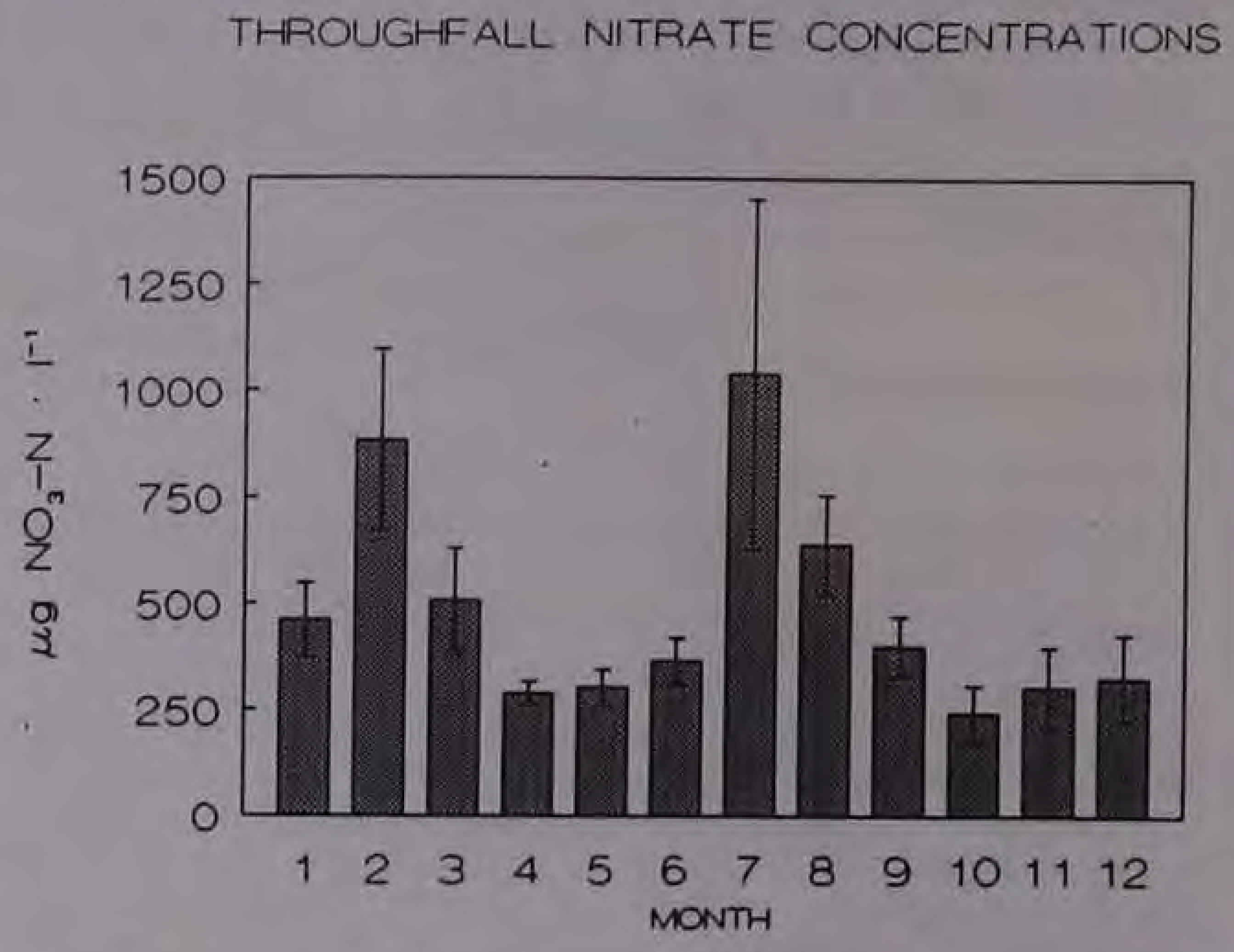

Figure 2. Average monthly nitrate concentrations in throughfall for 1982-1989, collected from soil surface samplers placed beneath unburned tallgrass prairie.

Results of the herbicide, nitrogen, and carbon additions on lysimeter volume and nitrate and ammonium concentrations are shown in Table 1. Only nitrogen additions and herbicide treatment significantly affected soil-water chemistry, and average values for these two treatments are reported in Table 2. The death of plant roots did not significantly affect the volume of soil water collected, although the average volume collected beneath dead roots (401 ml) appeared larger than that of live roots (270 ml). Plant death resulted in significantly more nitrates to be collected in lysimeters (17,209 μg N.l-1 vs 291 μg N.l-1 for dead and live roots, respectively). The addition of ammonium nitrate fertilizer resulted in a significant pulse of nitrates through the soil (17,235 μg N.l-1 vs 262 μg N.l-1 for fertilized and unfertilized, respectively). Surprisingly, ammonium concentrations were not statistically affected by the main treatments, although an interaction between fertilizer addition and the status of roots was observed (Table 1). Higher ammonium concentrations were observed only on the fertilized, herbicide treatment.

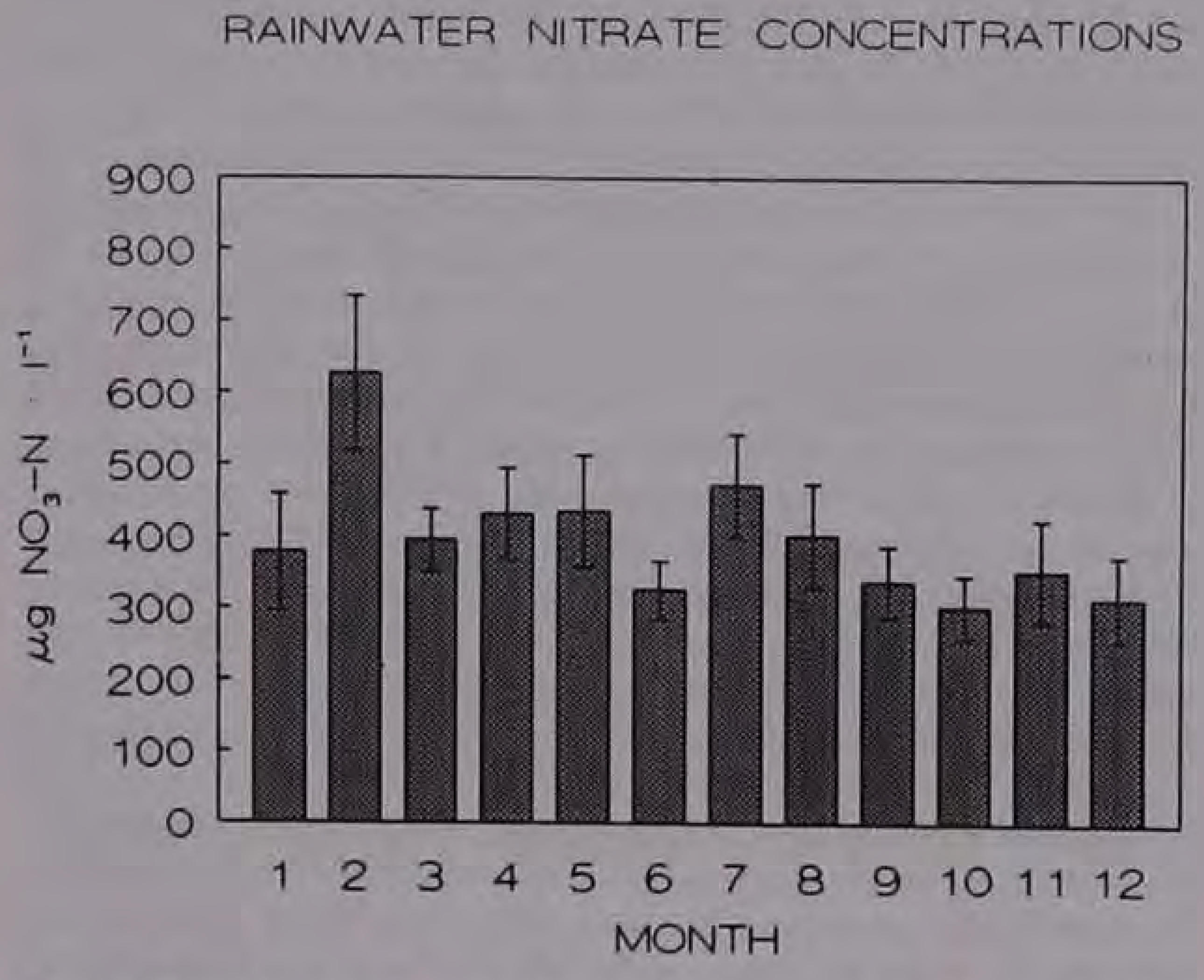

Figure 1. Average monthly nitrate content of rainwater for 1982-1988, obtained from the NADP wetfall collector.

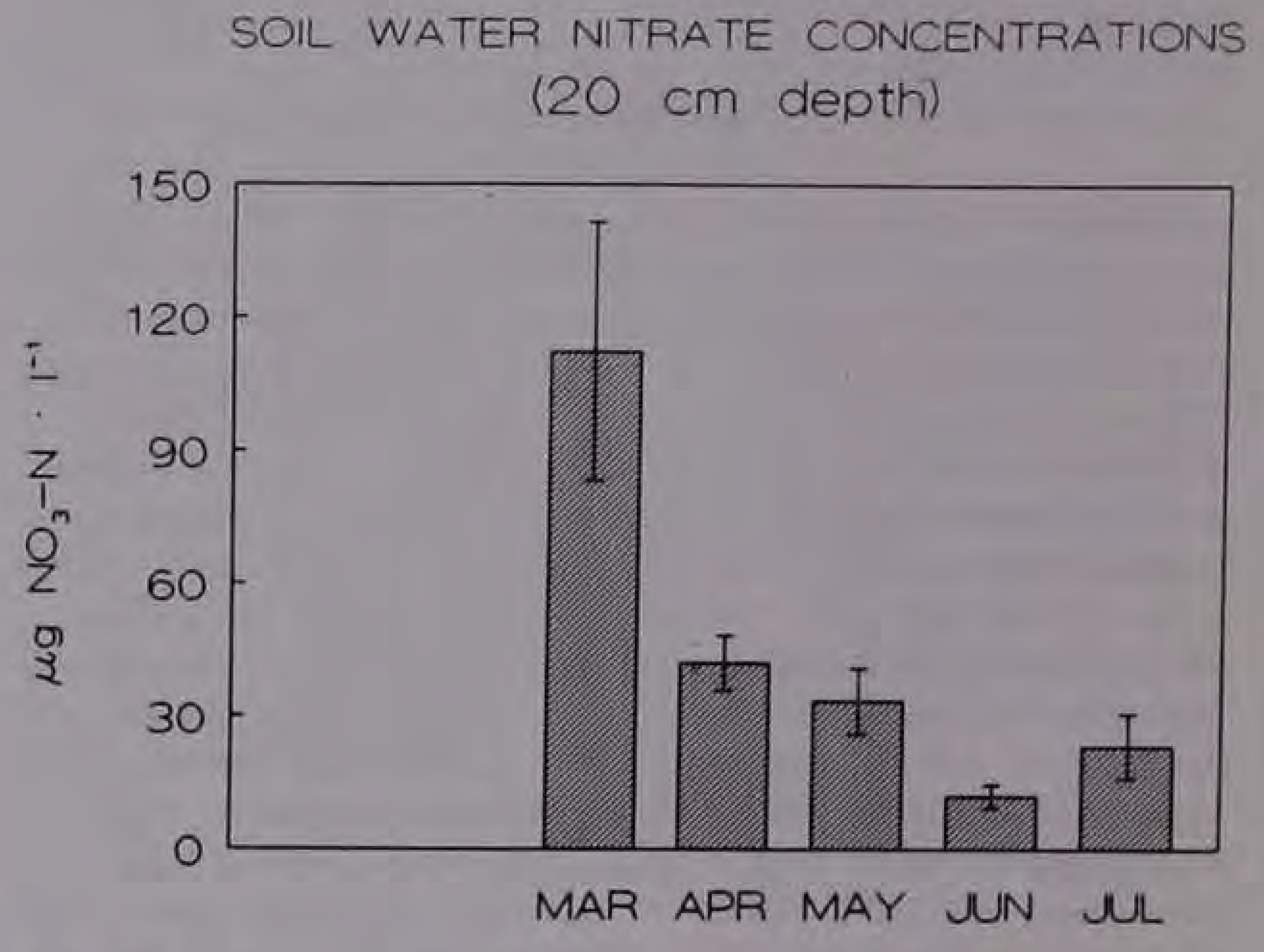

Figure 3. Average monthly soil water nitrate concentrations for 1982-1989, collected with porous cup lysimeters located at 20 cm depth.

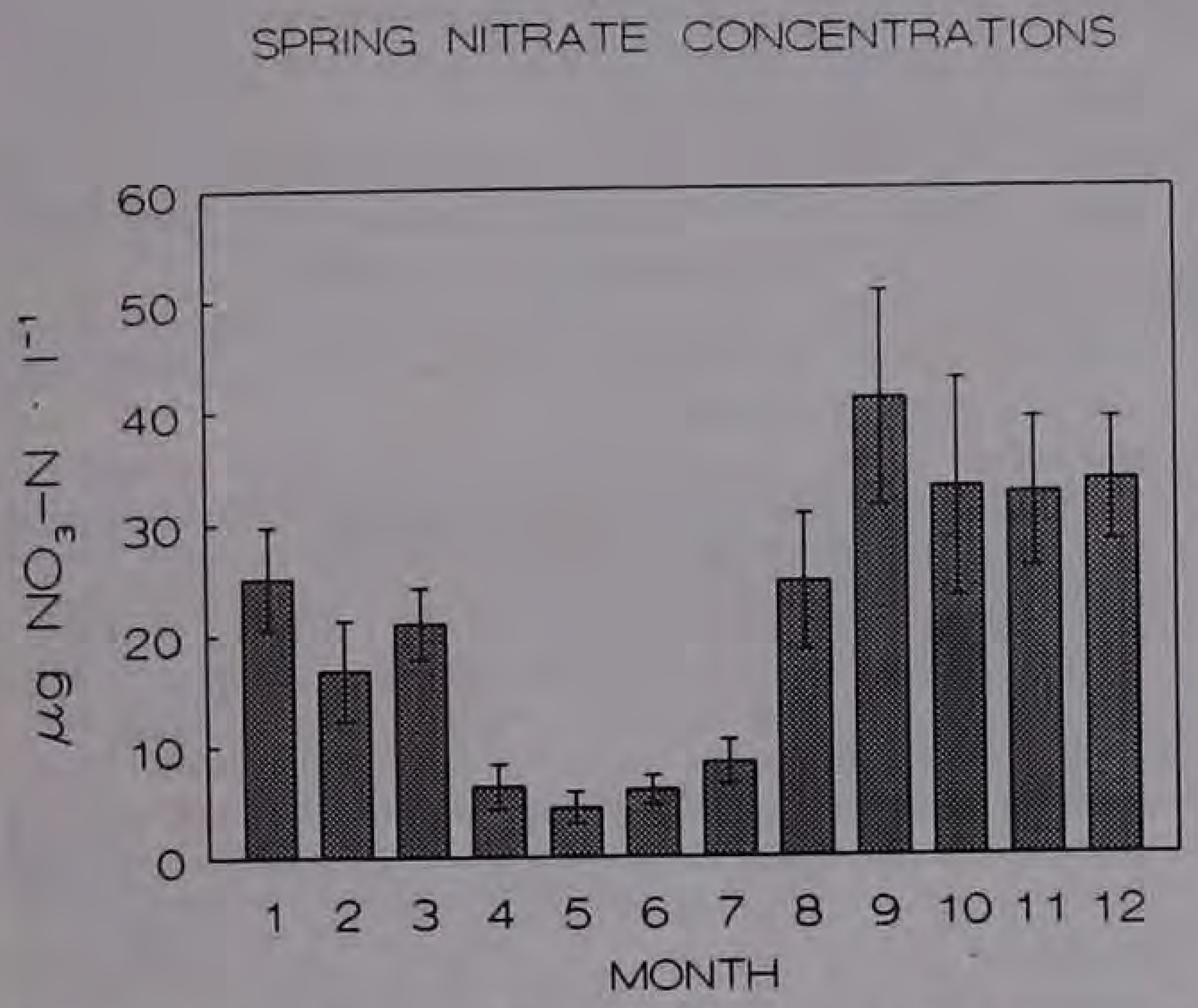

Figure 4. Average monthly spring (seep) nitrate concentrations for 1984. Values represent means and std errors of 4 springs.

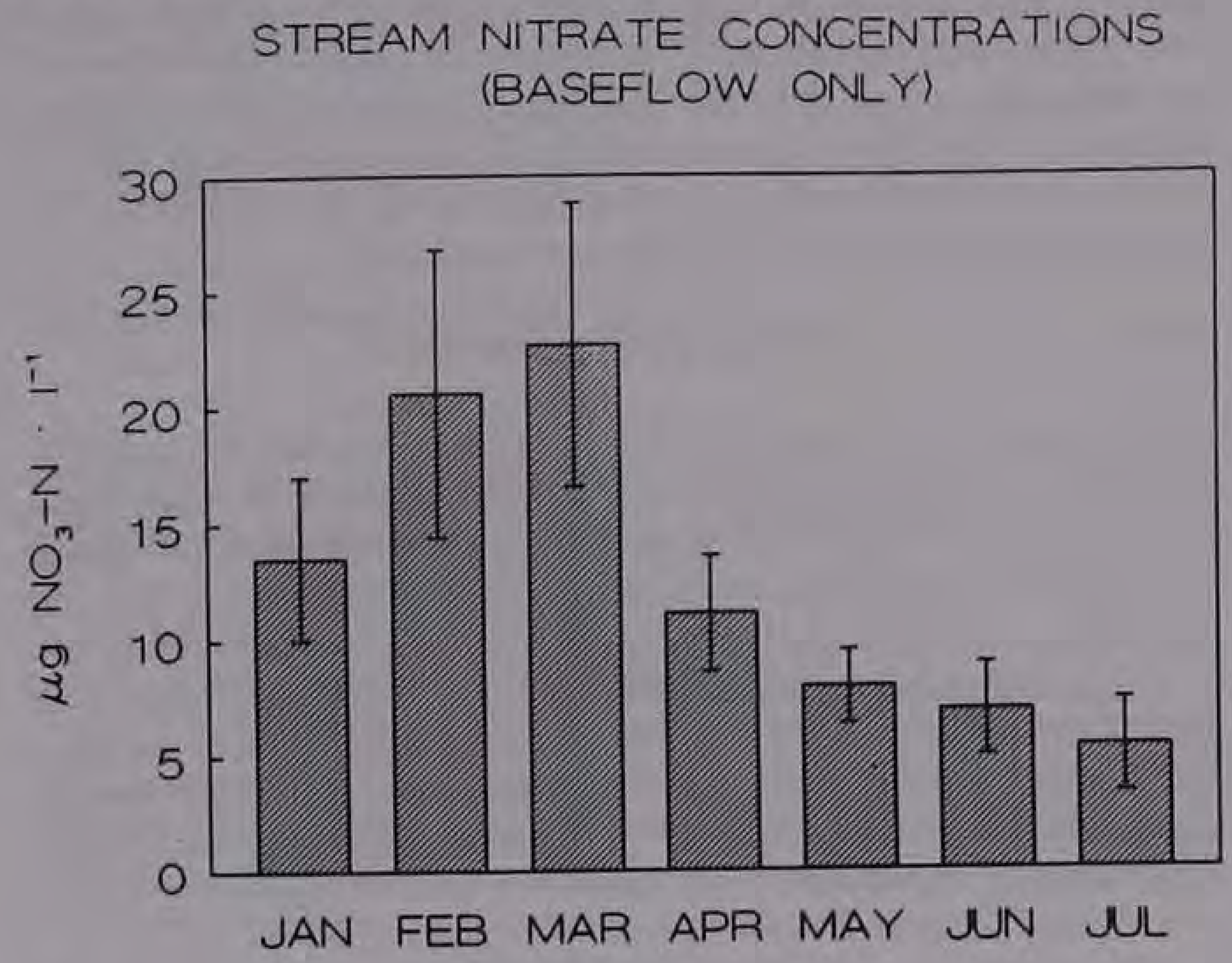

Figure 5. Average monthly stream baseflow nitrate concentrations for 1986-1989.

DISCUSSION

Ammonium-nitrogen concentrations in bulk precipitation, throughfall in burned prairie, and throughfall in unburned prairie sites average 456, 344 and 196 µg N.l-1, respectively, and follow a similar seasonal pattern as nitrate-nitrogen (Seastedt 1985). Despite the higher concentrations of ammonium in precipitation and throughfall, ammonium concentrations are seldom found in measurable amounts (<2 µg N.l-1) in either soil or stream water samples (Seastedt and Ramundo 1990, Tate 1990). This cation is either bound onto cation exchange sites, nitrified, assimilated by plants and microbes, or volatilized to ammonia gas. As shown here, even the addition of ammonium nitrate fertilizer does not result in measurable increases in ammonium at the 20 cm soil depth. In contrast, nitrate is highly mobile and, as demonstrated with the fertilizer experiment, can readily leach through the soils. In spite of this characteristic and the fact that native prairie soils contain large amounts of nitrogen, the tallgrass prairie soil-water and baseflow stream nitrate levels are among the lowest observed in North America (Tate, unpubl. results). Thus, the ability of the prairie to act as a nitrate filter deserves particular attention.

Baseflow nitrate levels of Konza Prairie streams are due, in part, to instream biological processes that continue to filter and remove inorganic nitrogen from the water (Tate 1990). Nonetheless, the chemical signature of stream water appears to mimic that of the soil water and springs, which, in turn, reflect the extent of plant root and microbial activity. Soil processes result in a reversal of the summer peak in concentrations of nitrate observed in throughfall.

Soil microbial activity can function as both a source and a sink for nitrate and, in a previous study (Seastedt et al. 1988), was shown to be capable of removing significant quantities of soil nitrates, provided a usable energy source was available. In the present study, however, we were unable to statistically demonstrate this effect by adding sugar to the soil surface. We suspect that the herbicide and fertilization treatments were of such a magnitude that effects of microbial immobilization processes were obscured.

The ability of the living root systems to absorb much of the fertilizer additions was readily evident from our results. Also, soil nitrate levels were about 10 times higher under unfertilized, herbicide treated plots compared to unfertilized controls (Table 2). The decomposition and mineralization of plant roots killed by the herbicide could have provided a source of the increased nitrates. However, soil-water measurements were made within one month of the death of the vegetation, and a previous root decay study demonstrated that net mineralization of decaying roots is delayed up to a year (Seastedt 1988). These findings are consistent with a variety of other local and regional studies demonstrating the importance of intact root systems in nutrient conservation processes (Spalding et al. 1988, Steichen et al. 1988, Hallberg 1986). The seasonality of root activity, therefore, appears to be driving the seasonality of baseflow water nitrates in Konza Prairie streams. Our results suggest that the restoration of

Table 1. Analysis of variables affecting soil water volume and chemistry.

Variable	*F-Value and significance level*[1]		
	Volume	*Nitrate*	*Ammonium*
Carbon (C)	0.29	1.03	0.06
Nitrogen (N)	1.06	18.00 ***	0.18
Herbicide (H)	0.53	10.47 **	0.42
C*N	0.62	0.00	0.84
C*H	0.55	2.70	0.25
N*H	0.00	2.44	4.88 *
C*N*H	1.91	2.70	1.30

[1] * p < .05, ** p < .01, *** p < .001

Table 2. Volumes (mls) and concentrations (µg N.l-1) of nitrate and ammonium collected by porous cup lysimeters.

Variable	*Controls*	*Treatment*		
		No herbicide Plus nitrogen	*Herbicide No nitrogen*	*Herbicide Plus nitrogen*
Volume	215 (73)	325 (119)	277 (79)	504 (182)
Nitrate	40 (23)	542 (475)	485 (442)	31,147 (8,222)
Ammonium	24 48 (12)	(4)	8 (3)	8 (20)

Note: Values are means of six samples with standard errors in parentheses.

native prairie grasses may be an important tool in addressing the groundwater-nitrate problem. Preserving the natural biodiversity of the tallgrass prairie provides an "ecosystem service" to society because the prairie acts as a nitrate filter by increasing plant participation in nitrogen retention, thus decreasing the enrichment of groundwater and streams with soil-derived nitrates.

ACKNOWLEDGEMENTS

This work was supported by a National Science Foundation Long-Term Ecological Research (LTER) grant to Kansas State University. Rainwater nitrate data were provided by the National Atmospheric Deposition Program, National Trends Network and were obtained from the Coordination Office, Natural Resources Ecology Laboratory, Colorado State University, Ft. Collins, CO 80523. Results presented here are from archived and documented Konza Prairie data sets. Information about these data can be obtained by contacting LTER Data Manager, Division of Biology, Kansas State University.

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SALT EFFECTS ON SEEDLING GROWTH OF SWITCHGRASS AND BIG BLUESTEM

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Abstract. Switchgrass (*Panicum virgatum* L.) and big bluestem (*Andropogon gerardii* Vitman) seedlings were grown for seven weeks in a greenhouse to measure their tolerance to salinity. Prior to planting, $CaCl_2$ was blended into soil mixtures to produce soils with 1.1, 6.5, 9.8, or 14.9 dS/m. Water measuring 0, 4, or 8 dS/m due to $CaCl_2$ additions was used to irrigate plots at 1.0, 1.25, 1.5, or 2.0 times field capacity. No seedlings survived seven weeks after planting when salinity of soil was 14.9 dS/m or water was 8 dS/m. Although soils remained moist throughout the trial, growth was suppressed for both grasses at all levels of added salinity. Salinity delayed emergence, decreased percent emergence, reduced seedling height, and reduced dry matter production of above- and below-ground tissue. As water amount increased, these decreases and reductions were less, primarily due to leaching of the $CaCl_2$. Saline water was more detrimental to grasses than was saline soil. Although switchgrass appeared slightly more tolerant of salinity than big bluestem, neither grass grew well even with slight salinity stress.

INTRODUCTION

Big bluestem (*Andropogon gerardii* Vitman) and switchgrass (*Panicum virgatum* L.) are important perennial warm-season grasses in the Great Plains. They are used frequently to revegetate tilled cropland and other disturbed sites. Although many soils in this region contain high levels of soluble salts, the germination and seedling growth response of these grasses to salinity is largely unknown. Objectives of this study were to determine the effect of salinity on seedling emergence and growth of big bluestem and switchgrass.

Dry matter yield of tops of switchgrass was reduced 71% when salt (NaCl) was applied in a 2.65 M solution to the soil surface in pots (Greub et al. 1985). As salt concentration of irrigation water increased the electrical conductivity (EC) from 1 to 4 decisiemens per meter (dS/m) and as the leaching fraction (ratio of amount of irrigation water to drainage water) decreased from .27 to .09, the annual dry matter production of tall fescue (*Festuca arundinacea* Schreb.) was reduced from 2 to 1.4 kg/m^2 (Hoffman et al. 1983). Ayers et al. (1943) and Wadleigh et al. (1946) found that increased irrigation frequency minimized salt damage on beans (*Phaseolus vulgaris* L.) and guayule (*Parthenium argentatum* Gray).

Excessive salt concentration in soil reduces water uptake by seeds and roots. Ions also may be absorbed in sufficient amounts to be toxic (Ayers and Hayward 1948). Alfalfa (*Medicago sativa L.*) seeds absorbed water less rapidly and Cl- accumulated more rapidly as the osmotic pressure of the substrate increased (Uhvits 1946). Roundy et al. (1985) found that germination and radicle length of basin wildrye (*Elymus cineru* Scribn. and Merr.) and tall wheatgrass (*Agropyron elongatum* (Host) Beauv.) decreased as osmotic potential of the germination medium became increasingly negative.

METHODS

Soil Preparation

Sharpsburg silty clay loam soil (fine montmorillonitic, mesic Typic Argiudoll) was ground and mixed with 25 kg of calcium carbonate per cubic meter of soil to raise soil pH to between 7.3 and 7.5 and to produce a soil with a high level of excess lime, which is common for many saline soils in Nebraska. Peat moss and vermiculite were mixed with the soil at 50% soil, 25% peat moss, and 25% vermiculite on a volume basis. This mixture was sterilized by steaming for five hours at temperatures reaching 95 C.

Soil Salinization

The amount of calcium chloride ($CaCl_2$) needed to produce soil mixtures with EC levels of 0, 4, 8, and 16 dS/m was estimated using the correlation curve of the saturation extract conductivity with the percent salt content for various soil saturation percentages (Richards 1954). Calcium chloride was used because many saline soils in the region are calcareous. For the soil mixture used in this investigation, the saturation percentage was 38, determined by the method of Longenecker and Lyerly (1964).

The $CaCl_2$ was added to soil in each pot individually. For each pot, one kilogram of soil mixture was spread on a polyethylene sheet, moistened by sprinkling with a salt solution containing 35 ml of distilled water and 1.0, 1.8, or 3.5 g of $CaCl_2$, and thoroughly mixed. Samples of these soil mixtures and of the mixture without added salt had actual EC's of 1.1, 6.5, 9.8, and 14.9 dS/m when 0.0, 1.0, 1.8, and 3.8 g of $CaCl_2$ were added, respectively. Soil then was placed in a 14 x 20 cm polyethylene pot lined inside with a polyethylene bag. The bottom of the bag was pulled through the central bottom hole of the pot and cut, allowing irrigation water to drain through while retaining soil in the pot.

Environmental Conditions

Pots were set on tables in a greenhouse. Maximum inside temperatures were 35 C (day) and 24 C (night). Minimum air temperatures were 29 C (day) and 16 C (night). A 14/10 hr day/night photoperiod was provided using eight 4000 w lamps placed 1.2 m above the canopy.

Seeding and Fertilization

On 11 Dec. 1984, a small quantity of soil was removed from each pot and reserved separately. The remaining soil was firmed. Ten seeds of debearded "Pawnee" big bluestem or "Pathfinder" switchgrass, tested at 84 and 71% germination, respectively, were placed on the soil surface. Seeds were lightly covered with the previously removed soil, and 1.4 g of phosphate, as triple super phosphate, was evenly broadcast on top of the soil.

Watering Procedure

Water salinity treatments consisted of distilled water or 4 and 8 dS/m solutions of $CaCl_2$ in distilled water.

Sixteen substitute pots, containing the same soil as the other pots except for no added salt, fertilizer, or seed, were placed among four blocks for measuring daily change in soil moisture. All pots were irrigated whenever average soil moisture of substitute pots reached 50% of field capacity (FC), which was expressed as moisture percent of soil samples on a dry-weight basis (Richards 1954).

Four amounts of irrigation water were used in this experiment—350, 437, 525, and 700 ml/pot—which represented 1.0, 1.25, 1.5, and 2.0 x FC, respectively. All pots were top watered the same day. Substitute pots were treated similarly to other pots but received only 350 ml of distilled water.

Data Collection and Analysis

Seedling emergence, plant height, and plants per pot were recorded weekly for seven weeks. Plant height reported was an

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arithmetic average of all live plants in the same pot. At the end of the experiment, soil samples were collected and composited from all pots that received the same treatment combination, and salinity was measured.

Four levels of soil salinity, three levels of water salinity, and four quantities of irrigation water were applied to each grass species in a complete factorial using four replicates in a randomized complete block design. Blocks were arranged within the greenhouse perpendicular to a potential temperature gradient caused by outside air intake and flow. Analyses of variance were calculated using the GLM procedure of SAS (1985).

RESULTS AND DISCUSSION

Neither switchgrass nor big bluestem emerged when soil salinity was 14.9 dS/m or when irrigated with saline water of 8 dS/m. All treatment combinations containing either of these materials were deleted from data analyses and will not be discussed further.

Emergence

Calcium chloride delayed emergence four to seven days (data not shown) and reduced emergence percentage of both switchgrass and big bluestem. Big bluestem emerged more rapidly and had a higher total emergence than switchgrass, possibly due to higher seed germinability and removal of dormancy by debearding.

Seedling emergence declined as soil salinity increased, and saline irrigation water (EC = 4 dS/m) caused a greater decline in emergence than did salt-free water. Switchgrass emergence declined 19% and 39% as soil salinity increased to 6.5 and 9.8 dS/m, respectively, when using salt-free water, and it declined 35% and 53% with saline water (Figure 1). Big bluestem emergence declined 19% and 43% with salt-free water and 51% and 64% with saline water (Figure 2).

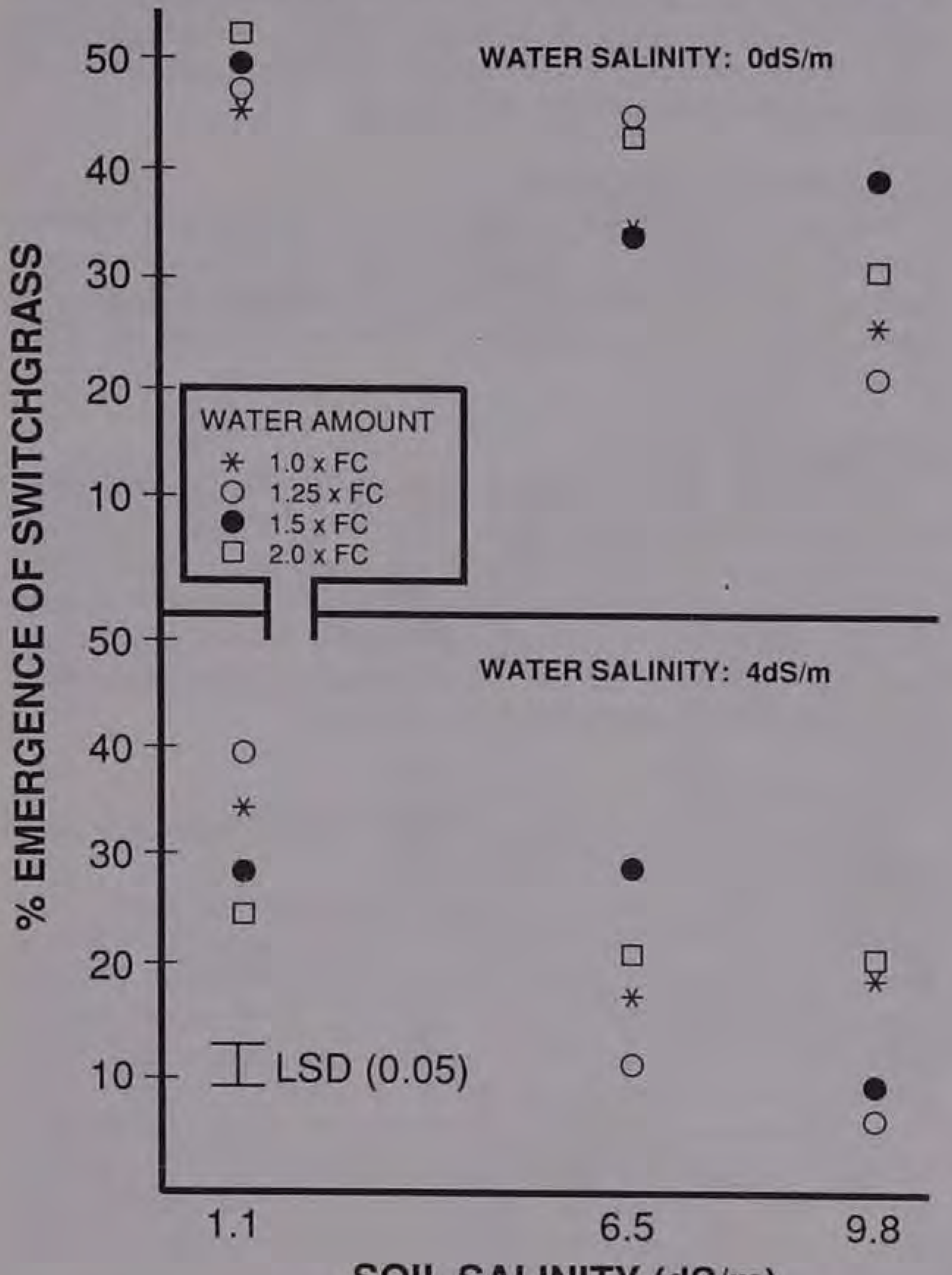

Figure 1. Effect of soil salinity, water salinity, and irrigation water amount (expressed as fraction of soil field capacity (FC)) on emergence of switchgrass.

Table 1: Electrical conductivity of the soil mixture after the seven week trial.

Irrigation water amount (fraction of field capacity)	*Initial soil salinity (dS/m)* 1.1		6.5		9.8	
	Water salinity (dS/m) 0	4	0	4	0	4
1.0	1.3	15.3	3.9	18.4	4.9	10.2
1.25	1.1	14.7	3.5	9.1	4.5	8.3
1.5	0.7	11.0	3.1	9.2	5.3	9.2
2.0	0.7	14.6	1.2	10.8	1.2	4.5

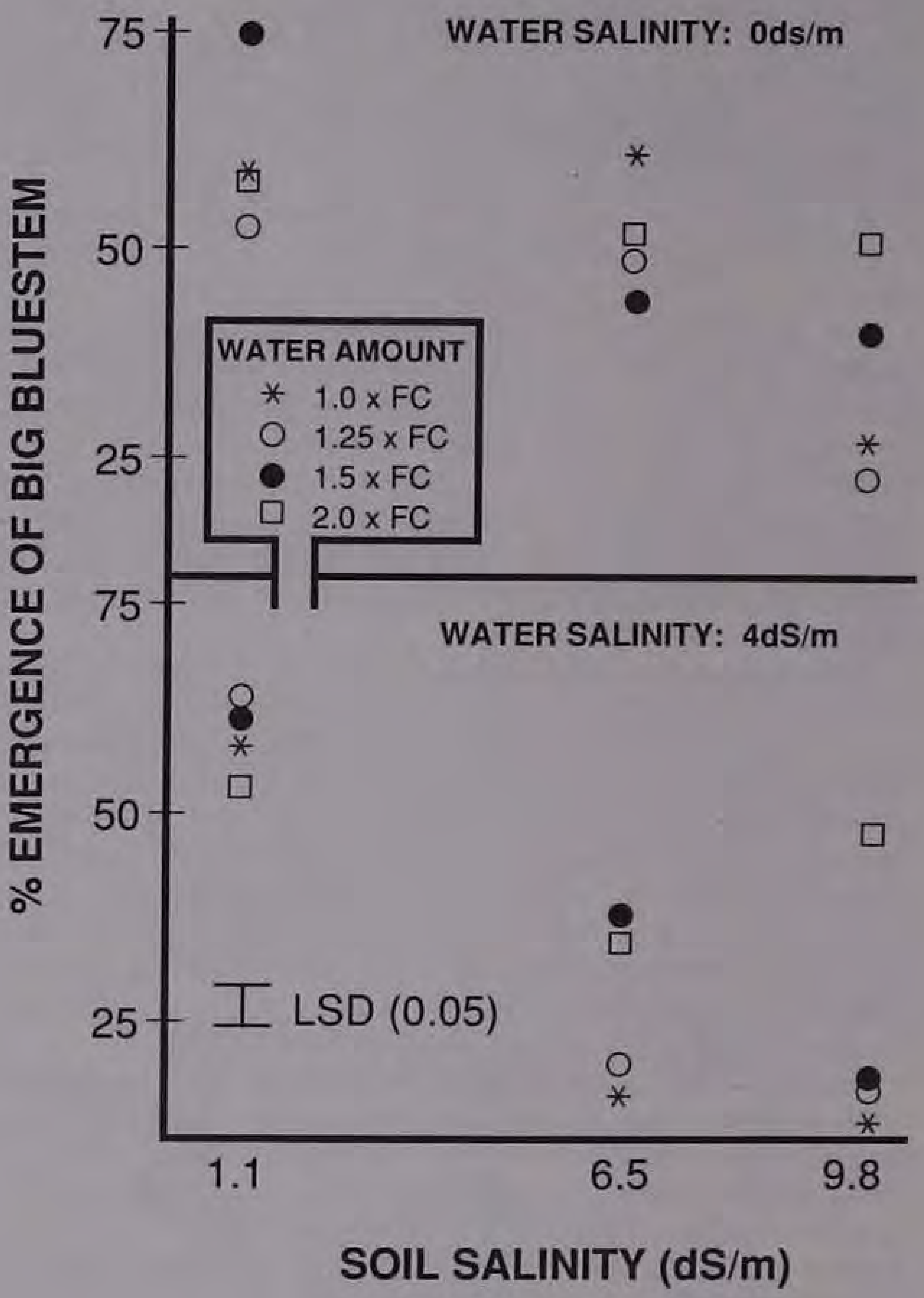

Figure 2. Effect of soil salinity, water salinity, and irrigation water amount (expressed as fraction of soil field capacity (FC)) on emergence of big bluestem.

A significant water amount by soil salinity interaction resulted because soil salinity depressed emergence less as irrigation water amount increased. This implies that salt was leached from the germination and emergence soil zone as water passed through the soil, permitting more emergence. Lower soil salinity was measured at the end of the trial in soils receiving higher amounts of irrigation water (Table 1).

Table 2: Plant height, above-ground dry matter yield, and crown-plus-root dry matter yield of "Pathfinder" switchgrass seven weeks after planting as influenced by soil and water salinity and amount of irrigation water.

		Soil salinity (dS/m)					
	Irrigation water amount (fraction of field capacity	1.1		6.5		9.8	
		Water salinity (dS/m)					
Response		0	4	0	4	0	4
		cm					
Plant height	1.0	37	15	36	8	9	4
	1.25	36	26	32	4	18	4
	1.5	21	27	36	22	24	0
	2.0	30	29	37	23	25	19
		g					
Above ground yield	1.0	2.01	0.64	1.54	0.09	0.42	0.10
	1.25	2.86	1.30	2.50	0.16	0.41	0.03
	1.5	2.36	1.46	2.18	0.48	2.06	0.00
	2.0	2.36	1.35	1.65	0.38	1.36	0.48
		g					
Yield of crown + roots	1.0	1.5	0.15	0.84	0.13	0.36	0.70
	1.25	2.02	0.51	1.37	0.07	0.27	0.00
	1.5	1.56	0.70	1.19	0.12	1.38	0.00
	2.0	1.45	0.75	1.07	0.24	0.78	0.23

LSD(0.05) =13 cm, 0.96 g, and 0.61 g for plant height, above-ground yield, and yield of crown + roots, respectively.

Plant Height

Plant height one week after planting was omitted from the analyses to improve homogeneity because germination of grass seeds receiving high salinity treatments was delayed about one week. Stage of development and number of plants in some pots were not constant because some plants died due to salinity stress, and some plants emerged after inhibition by salt was removed by leaching. Therefore, plant height was not uniform within each pot and was averaged.

Plant height was reduced by saline soil and irrigation water, and the amount of reduction increased as salinity stress increased (Tables 2 and 3). Plants grown in soil with an initial EC of 9.8 dS/m showed reduced growth compared with plants grown in non-saline soil following irrigation with salt-free and saline water. Switchgrass plants were more than 30% shorter while big bluestem plants were more than 70% shorter.

Seedlings in saline conditions generally grew taller as the amount of irrigation water increased. Wetter soil is needed to reduce salinity effects on plants as salt concentration increases (Donahue et al. 1983). A water salinity by water amount interaction ($p < .10$) indicated that more irrigation was needed with saline than with salt-free water. Low amounts (1.5 x FC or less) of saline

Table 3: Plant height, above-ground dry matter yield, and crown-plus-root dry matter yield of "Pawnee" big bluestem seven weeks after planting as influenced by soil and water salinity and amount of irrigation water.

		Soil salinity (dS/m)					
	Irrigation water amount (fraction of field capacity	1.1		6.5		9.8	
		Water salinity (dS/m)					
Response		0	4	0	4	0	4
		cm					
Plant height	1.0	28	17	19	5	10	2
	1.25	27	22	22	13	14	3
	1.5	30	19	24	14	23	6
	2.0	29	20	28	17	30	21
		g					
Above ground yield	1.0	1.34	0.51	0.39	0.00	0.31	0.00
	1.25	1.99	1.31	1.56	0.06	0.37	0.03
	1.5	2.32	0.53	1.14	0.15	0.77	0.37
	2.0	1.87	0.85	1.90	0.25	1.97	0.94
		g					
Yield crown + roots	1.0	1.47	0.23	0.77	0.00	0.23	0.00
	1.25	1.98	0.66	1.45	0.03	0.31	0.00
	1.5	2.47	0.29	1.08	0.03	0.94	0.15
	2.0	2.63	0.80	1.82	0.08	1.47	0.40

LSD(0.05) =9.2 cm, 0.7 g, and 0.8 g for plant height, above-ground yield, and yield of crown + roots, respectively.

water often increased soil salinity while irrigation with salt-free water lowered soil salinity (Table 1).

Dry Matter Production

Dry matter yields of switchgrass and big bluestem declined as soil salinity increased (Tables 2 and 3). When salt-free water was used for irrigation, the average above-ground yield of switchgrass grown in moderate (6.5 dS/m) and high (9.8 dS/m) salinity soil was 82% and 45%, respectively, of the yield in non-saline soil. Big bluestem yields were 64% and 45% of yields in non-saline soil, respectively.

Above-ground dry matter yields of switchgrass and big bluestem irrigated with saline water averaged less than one-half the yield from non-saline irrigation in non-saline soils (1.1 dS/m). When both soil and irrigation water were saline, most above-ground yields were less than 10% that of non-saline yields.

For both switchgrass and big bluestem, crown and root production tended to be reduced more by increased soil or water salinity than was above-ground yield. In addition, both grasses tended to produce higher dry matter yields at 1.5 and 2.0 x FC than at lower amounts of irrigation water, especially under saline conditions.

CONCLUSIONS

Switchgrass tended to be affected slightly less than big bluestem by saline soil or water. However, growth of both grasses was substantially reduced even in soils with slight salinity (6.5 dS/m). Because watering procedures in this study maintained moist soils over a longer period of time and caused more leaching than is generally experienced under rainfed conditions in the Great Plains, reduction in growth due to salinity is likely to be greater in natural environments. Thus, neither switchgrass nor big bluestem should be used to establish vegetation on sites that will cause any more than very slight salinity.

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DISEASES OF BIG BLUESTEM CAUSED BY SMUT FUNGI

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Abstract. Big bluestem, *Andropogon gerardii*, is commonly found in Iowa prairie areas. Members of some bluestem populations are parasitized by one of two different species of smut fungi. Both fungi cause systemic, perennial disease, and infected bluestem plants may be severely stunted and prevented from reproducing. Culm smut results from infection by *Sorosporium provinciale*, which causes entire inflorescences to be converted into large galls containing teliospores. Kernel smut, caused by *Sphacelotheca occidentalis*, is characterized by the presence of galls that replace the individual bluestem seeds and contain teliospores. Culm smut has been known from southern Iowa for many years. Kernel smut was first reported in Iowa in 1978, and since that time, it has consistently been found in native prairies in northwest Iowa and planted prairies in central Iowa. We are monitoring the presence of these fungi on a number of native and restored prairies.

INTRODUCTION

Big bluestem (*Andropogon gerardii* Vitm.) dominates much of the Iowa tallgrass prairie in both stature and coverage; healthy plants may reach 2 m in height, and populations may cover many square meters. Big bluestem often grows in extensive stands along roadsides and is found in most restored and planted prairie areas, as well as in native prairies.

For the past several years, we have observed a gradual decline of plant vigor and number in some big bluestem populations in Iowa. This decline is correlated with the presence of one of two species of smut fungi that parasitize big bluestem. The two fungal species, *Sorosporium provinciale* (Ell. and Gall.) Clint. and *Sphacelotheca occidentalis* (Seym.) Clint., are related members of a group of basidiomycetes known as the smut fungi. Both species are systemic perennial pathogens, and both form teliospores in gall-like sori that form in host inflorescences. Teliospores are transported by wind and water, and probably initiate new infections when they germinate near emerging bluestem tillers or seedlings. Infected plants are not only prevented from reproducing by seed, but they may also be dramatically stunted.

The two disease-causing fungi differ in the location of the sori they produce and in certain details of sporogenesis. Sorus development and sporogenesis in these fungi have been described previously (Snetselaar and Tiffany 1990, 1991). Our observations of diseased plants in naturally infected populations of big bluestem in Iowa are the focus of this paper.

MATERIALS AND METHODS

Data on disease distribution were compiled from collections in the Ada Hayden Herbarium at Iowa State University and from samples collected by the authors and other individuals.

Several diseased bluestem populations were located in June 1987. Some populations were marked with a central, metal stake, and individual diseased plants were then located by recording a distance and compass bearing from the central point. Small, numbered, metal tags on wires were pushed into the ground at the base of each plant. Plots were revisited in the summers of 1988 and 1989.

A permanent plot was established at Cayler Prairie in 1987 in a bluestem population infected with *S. occidentalis*. The center of the plot was marked with a metal stake, and four smaller stakes were placed at right angles to each other 15 m from the center. Diseased and healthy plants were tallied in the cross-shaped plot formed by stretching a metal tape from the center to each of the outside stakes and moving a 3/4 meter quadrat along the tape. Diseased and healthy culms were counted in each quadrat.

Histological and cytological methods were described elsewhere (Snetselaar and Tiffany 1990, 1991).

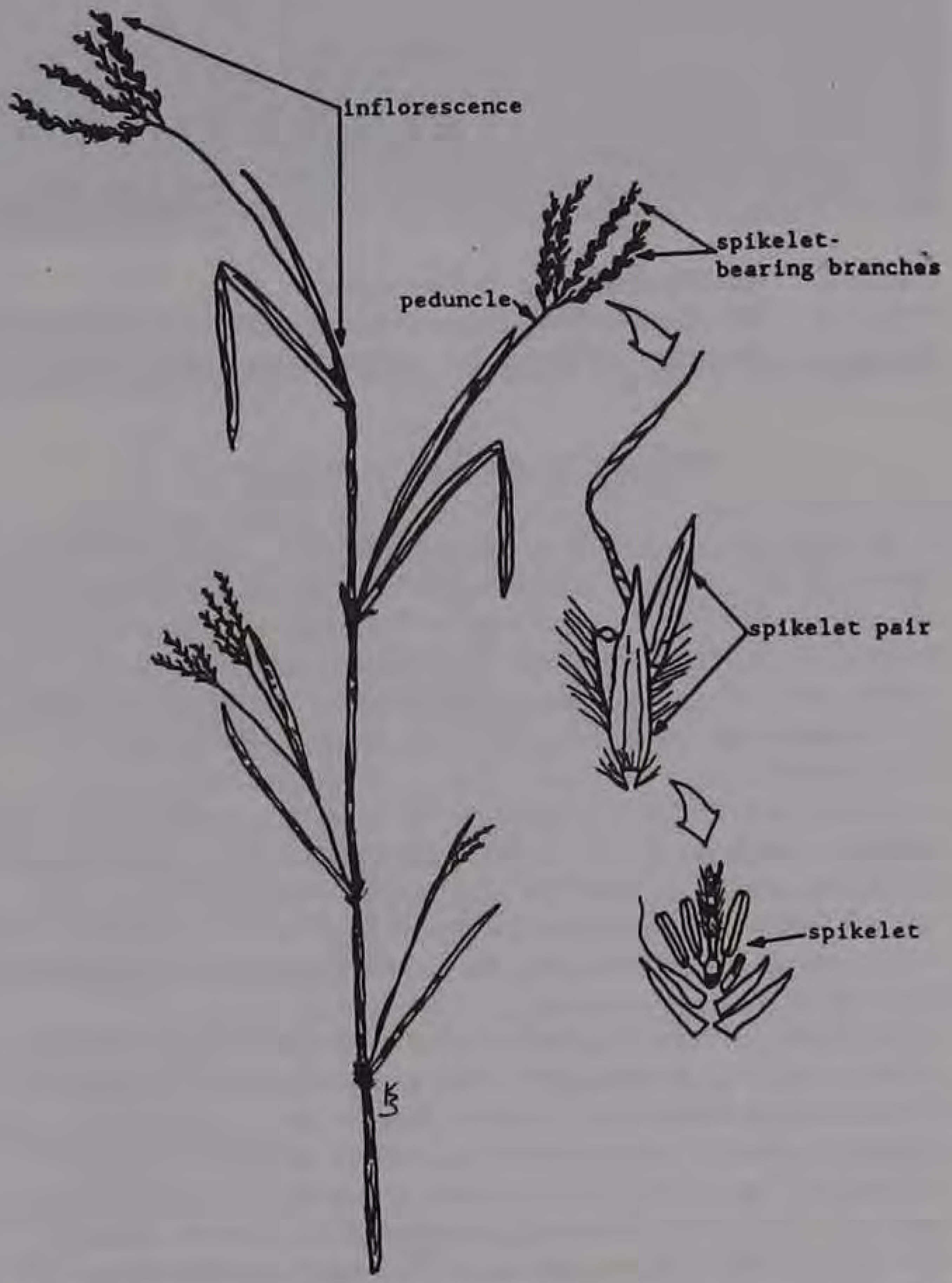

Figure 1. Flowering culm of big bluestem, *Andropogon gerardii*.

Figure 2. **Healthy bluestem inflorescence.**
Figure 3. **Bluestem inflorescence infected with *Sorosporium provinciale*. Sorus has ruptured to release spores (arrow).**
Figure 4. **Bluestem infloresence infected with *Sphacelotheca occidentalis*. Sori are found in sessile and stalked spikelets (arrows).**

OBSERVATIONS AND DISCUSSION

Sorosporium provinciale causes a disease called culm smut (Durán 1987), although it is actually the individual inflorescences of big bluestem that are converted into single smut galls that may be several cm long (Figures 1-3). Infected culms are precocious, bearing sori initially enclosed by leaf sheaths but eventually emerging and releasing spores several weeks before healthy plants produce flowers.

Culm smut has been reported from Iowa for a number of years and seems to be confined to the southern part of the state (Figure 5). It also occurs in nearby prairie states, including Kansas, Missouri, Nebraska, and Indiana (Fischer 1953, Farr et al. 1989). Two recent central Iowa collections were made from restored prairies in state parks.

We have been following a diseased bluestem population at a restored prairie in Ledges State Park in Boone County since 1987. Disease has been present in the same location every summer, including one year when controlled spring burning of the prairie occurred. The disease seems to be increasingly prevalent in the area, and big bluestem coverage appears to be reduced. However, although diseased plants marked in 1987 were also diseased in the following two years, we cannot be certain whether the increased disease occurrence is due to infection of healthy plants via teliospores, increased tillering in diseased plants, or other causes.

Sphacelotheca occidentalis causes kernel smut disease of big bluestem. Kernel smut was first reported from Iowa in 1978 (Knaphus and Tiffany 1986), although there are earlier records from Nebraska and Kansas (Zundel 1930, Dunleavy 1956). *Sphacelotheca occidentalis* has been collected numerous times from various locations in the northern half of Iowa since the first report (Figure 6). We visit a number of these prairies annually, and it seems to us that in some sites the proportion of diseased plants is increasing as the total amount of bluestem present is decreasing. We are attempting to extend and quantify these observations.

The permanent plot was established at Cayler Prairie in northwest Iowa as a preliminary effort to determine how rapidly kernel smut might be spreading through an area. The site chosen contained both diseased and healthy plants; 488 healthy culms and 447 diseased culms were counted in the cross-shaped plot in July of 1987. Culms were not counted in 1988 and 1989 because very few bluestem plants flowered. These were exceptionally dry years, and, presumably, the drought conditions were involved in the lack of floral production. Wetter conditions existed in 1990, and flowering occurred. Culms were counted in mid-August; 13 healthy and 151 diseased culms were found. We observed some additional vegetative bluestem plants, but the total bluestem population appeared to have been reduced during the three years. It is not possible to draw firm conclusions from this preliminary study, but the results suggest that further investigations might be of interest to bluestem breeders and prairie restoration workers, as well as biologists studying prairie plant communities.

We have made additional observations of plants infected with kernel smut that could be pertinent to subsequent studies. Like *S. provinciale*, *S. occidentalis* has systemic, perennial mycelium that can be found in various parts of infected plants (Snetselaar and

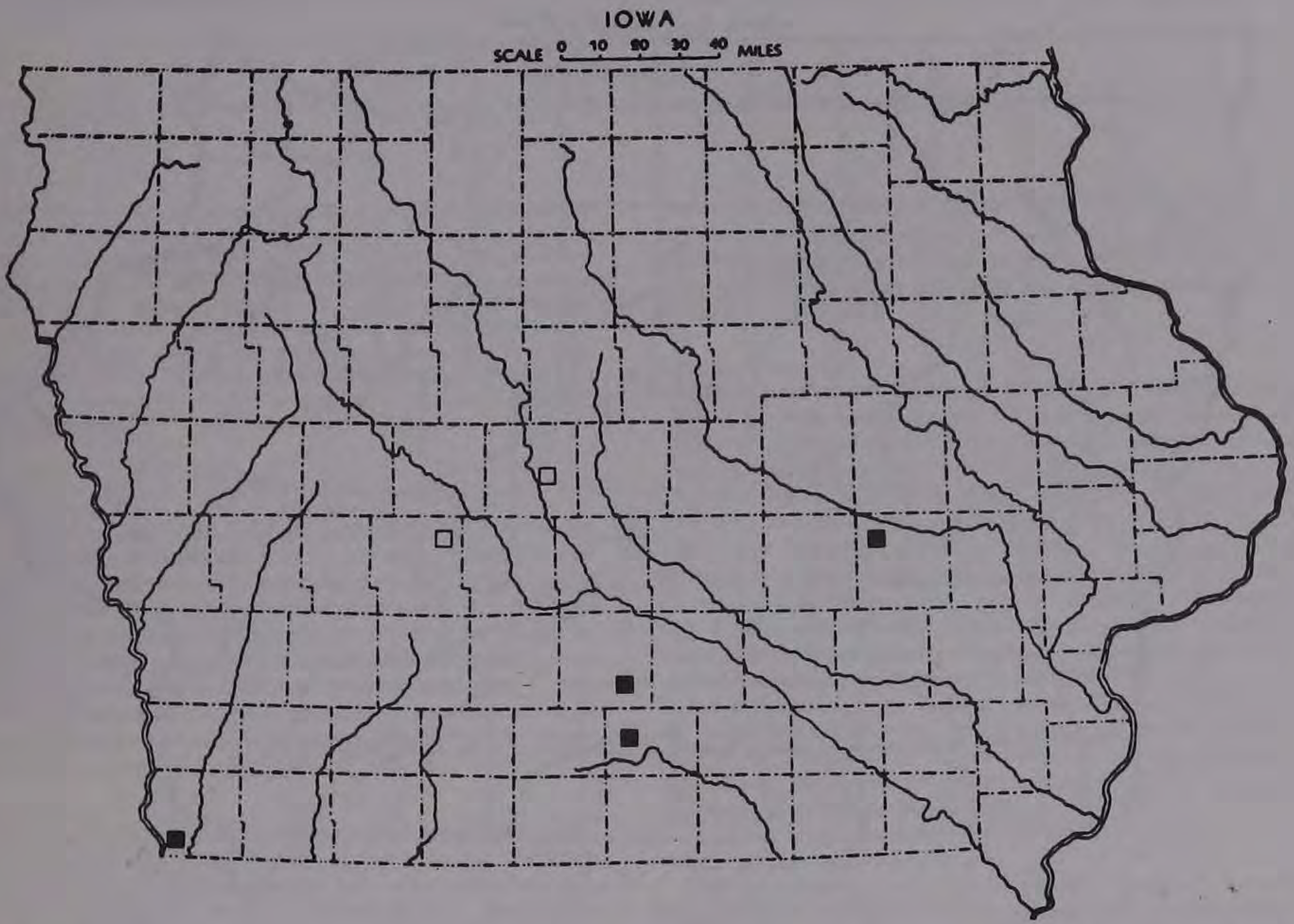

Figure 5. Collections of *Sorosporium provinciale* in Iowa. Solid symbols represent collections from native stands; open symbols indicate restored grasslands.

Tiffany 1991). Once plants are infected, culms produced in succeeding years are also potentially smutted. We observed, however, that some plants produce healthy as well as diseased inflorescences. We observed one clump of big bluestem in a garden prairie for several years, and in at least one year, it produced apparently normal flowers early in the season and smutted flowers later in the year. These plants were not noticeably stunted and the inflorescences were less uniformly smutted than those we observed on more severely stunted plants from native prairies. In addition, the few smut galls produced were extremely large.

Lack of stunting and scattered, large smut galls were observed in bluestem at a number of sites; these were almost always areas where bluestem had been recently planted. Perhaps these features are characteristic of recently infected plants. It is also possible that some genotypes of big bluestem are more tolerant to smut infection than others. Infected tolerant plants may suppress sporulation in some way. Disease has been present in Kansas and Nebraska, states where most bluestem seed is currently produced, for many years. There may have been selection, in nature or by breeders, for genotypes of bluestem more resistant or tolerant to fungal infection.

Big bluestem spikelets are borne on the inflorescence branches in pairs; the sessile spikelet is perfect, and the stalked one is normally male (Figure 1). Galls formed by *S. occidentalis* range in length from a few mm to over 1 cm and develop between the glumes of both sessile and stalked spikelets (Figure 4). We observed that galls were often made up primarily of infected tissue of the axis supporting the floral organs; atrophied stamens, ovary and stigmas were found at the apices of sori taken from both sessile and stalked sori. The presence of atrophied ovaries in stalked spikelets suggests that infection may stimulate production of plant parts that would not normally be present. Production of extra floral organs has been reported for other plants infected by smut fungi (Hansing and Lefebvre 1941, Fischer and Holton 1957).

It has also been reported that big bluestem plants from some populations frequently produce seed in the stalked spikelets (Boe et al. 1983). We noticed that sparsely smutted culms from some planted bluestem populations frequently produced viable seed in stalked spikelets. Correlation between smut fungal infection and seed production in pedicellate spikelets cannot be made at this time, but the possibility of a link may be of interest to breeders.

The severe reactions of big bluestem plants in native prairies in northwest Iowa may be an indication that these plants have not been previously exposed to the smut fungus. Imported bluestem seed may be the source of smut spores. Perhaps out-of-state big bluestem has been selected for resistance or tolerance to the smut fungus, either naturally or by bluestem breeders. The current "epidemic" provides an opportunity to follow disease progress in a more-or-less undisturbed grassland community.

Native midwestern prairies survive primarily as small remnants. We know little about the long-term impact of disease on these plant communities, although there is evidence that management practices may affect the incidence of fungal disease on prairies (Shearer and Tiffany 1989). Disease-causing fungi may be agents of change over time in the "mix" of plants present in scattered prairie rem-

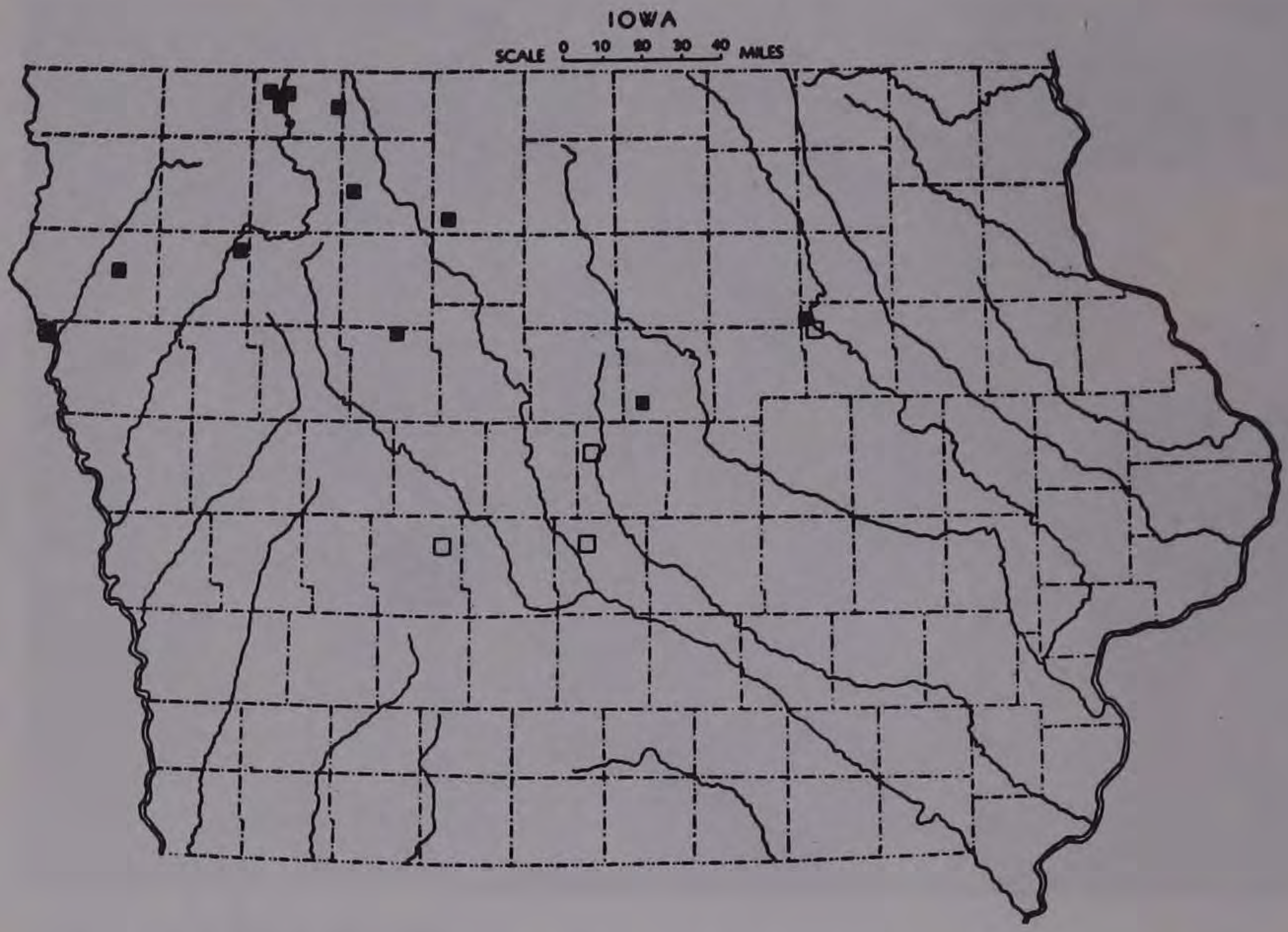

Figure 6. Collections of *Sphacelotheca occidentalis* in Iowa. Solid symbols represent collections from native stands; open symbols indicate restored grasslands.

nants. These changes are not necessarily detrimental to the prairie communities; diversity may increase when the coverage of dominant plants, such as big bluestem, is reduced, provided that a seed source for other native plants is nearby and not overwhelmed by seeds from exotic species.

ACKNOWLEDGEMENTS

This study was funded in part by the Graduate College at Iowa State University. Additional funds and facilities were provided by Iowa Lakeside Laboratory, and we particularly thank Dr. R. V. Bovjberg and Mark and Judy Wehrspann of that institution. We are grateful to those who contributed collections of diseased bluestem, and to Dr. G. Knaphus for field assistance.

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PROPAGATION OF SHOOTING STAR, *DODECATHEON MEADIA*

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Abstract. Studies on the propagation of shooting star, *Dodecatheon meadia*, reveal that the species requires five to six years to reach flowering from the seedling stage under normal field conditions. Laboratory and greenhouse procedures employed to shorten this long maturation include manipulation of photoperiod and application of gibberellins. Twenty-four hour illumination may circumvent the ephemerality associated with field conditions, as does the use of gibberellins applied during the seedling (cotyledon) stage. Propagation of mature plants by separating and replanting suppressed buds remains one of the most reliable—though labor intensive—means for increasing the species for small-scale grassland restorations.

INTRODUCTION

The common and much-loved shooting star, *Dodecatheon meadia L.*, of open woodlands and plains in the upper Midwest has the reputation of a species difficult to propagate for the purposes of prairie restoration. Its small seeds, long maturation period (Figure 1), and brief period of annual growth combine to thwart the patience of workers accustomed to more hasty development typical of some species, such as the robust prairie Asteraceae. In this report, I summarize the life cycle of shooting star, review the literature on its biology, and present the results of my efforts to shorten the long period of development from seed to flower.

Life Cycle

Shooting star belongs to the group of plants we call the spring ephemerals (Sörensen 1984). About mid-March, or later depending on latitude, the buds formed during the previous spring break dormancy as a consequence of winter cold stratification. Leaves soon appear above the soil surface in clusters of small rosettes. They continue to elongate, depending upon the amount of litter through which they must protrude, until about mid-April when the flower buds begin to show in the center of the rosette. Soon, the leafless flower stalk (the scape) begins to elongate, and the earliest flowers reach anthesis in early May. Peak of flowering in our area (northern Illinois) occurs fairly reliably by 10 May each spring. Young fruits develop by late May, coinciding with the gradual senescence of the leaves. By mid-June, the leaves have withered entirely, leaving behind only the slowly maturing, achlorophyllous fruiting scape (Figure 1), and the below-ground bud that remains dormant through the growing season and the following winter. Capsules rupture at the summit of the fruit by late July, and by mid-August, all are fully open. As the stiff peduncle is whipped about by wind and animal movements, seeds disperse through the opening of the erect capsule summit. However, one may often find seeds remaining in the capsule on scapes still standing the following spring. Crushing the dry capsule frequently produces an additional yield of undispersed seeds. Under natural conditions, seeds probably germinate in the spring, about the same time buds of established plants break dormancy, but a significant number may germinate in the fall if an early, brief cold period is followed by a warm spell. Whether such seedlings survive the rigors of winter remains unknown. The available literature lacks information on seedling survival (population recruitment) under natural conditions.

METHODS AND RESULTS

The remarks which follow are based on experiments and observations conducted in a laboratory and greenhouse on seeds and plant parts derived from plants of two extensively cloned individuals, which have been in cultivation for many years. Seeds gathered from these plants constitute the source for germination tests, and root material from mature specimens of them have been used for additional experiments.

Seed Germination

Moist stratification of seeds, under artificial as well as natural conditions, seems routinely essential for germination (Greene and Curtis 1950). But workers have reported different lengths of time necessary for optimum results. Following the work of Threlfall (1970), and corroborated in the present study, one may obtain satisfactory germination percentages from as few as seven days of refrigeration in a moist medium at 5.0-10.0 C. Highest germination percentages resulted from a cold stratification duration of 21 days. Turner and Quarterman (1968) reported on the use of gibberellic acid (GA) combined with cold temperatures as a method to improve germination, but my experience suggests that the 21-day treatment obviates whatever benefit the use of GA confers. Individual seed batches seem to differ somewhat in their responses to the length of cold treatment, based upon a number of variables, such as age and water content of the seeds. In all seed-related experiments, the seeds were sorted beforehand in a "fan" to eliminate empty or poorly-developed seeds.

From Seedlings to Flowering Plants

With germination of the seed, a hypocotyl emerges to develop into a soft-tissued taproot. Concommitantly, the epicotyl arises, and the two orbicular cotyledons enlarge to a maximum diameter of about 6.0 mm. During the first season, as observed under greenhouse culture, further development takes place solely beneath the soil surface. The first organ to develop is a fleshy lateral root. A small bud forms at the juncture of the lateral root and the initial taproot. The bud enlarges to about 2.5 mm. As the season progresses, the fleshy lateral root continues its elongation to a total of about 4.0 cm, depending upon local growing conditions of light, moisture, and soil fertility. By this time (mid-June), the slender taproot and other tiny rootlets degenerate, and by late June, the only parts of the young plant remaining to carry it through until the following March are the vegetative bud and the fleshy lateral root (Figure 1, top panel).

The following year, the same sequence takes place, except that the aerial parts consist of the "young adult" or juvenile leaves that develop from the previous season's underground bud. During this second year of growth, the fleshy root system increases in size. A new bud forms, and the ephemeral, above-ground parts wither, leaving again only the fleshy roots and a bud to pass through the dormant period.

It has not been possible to observe a single plant pass through its entire developmental sequence from seedling to flowering, but from various observations, it appears that under field conditions a plant likely requires five to six years or longer of vegetative growth to reach the level of maturity necessary to produce its first inflorescence (Figure 1, bottom panel). My findings differ from those of Thompson (1953), who reports that "two or three years are required to raise flowering plants from seeds." However, he does not specify a particular species of *Dodecatheon*. Turner and Quarterman (1968) state that their experimental material failed to flower even after the

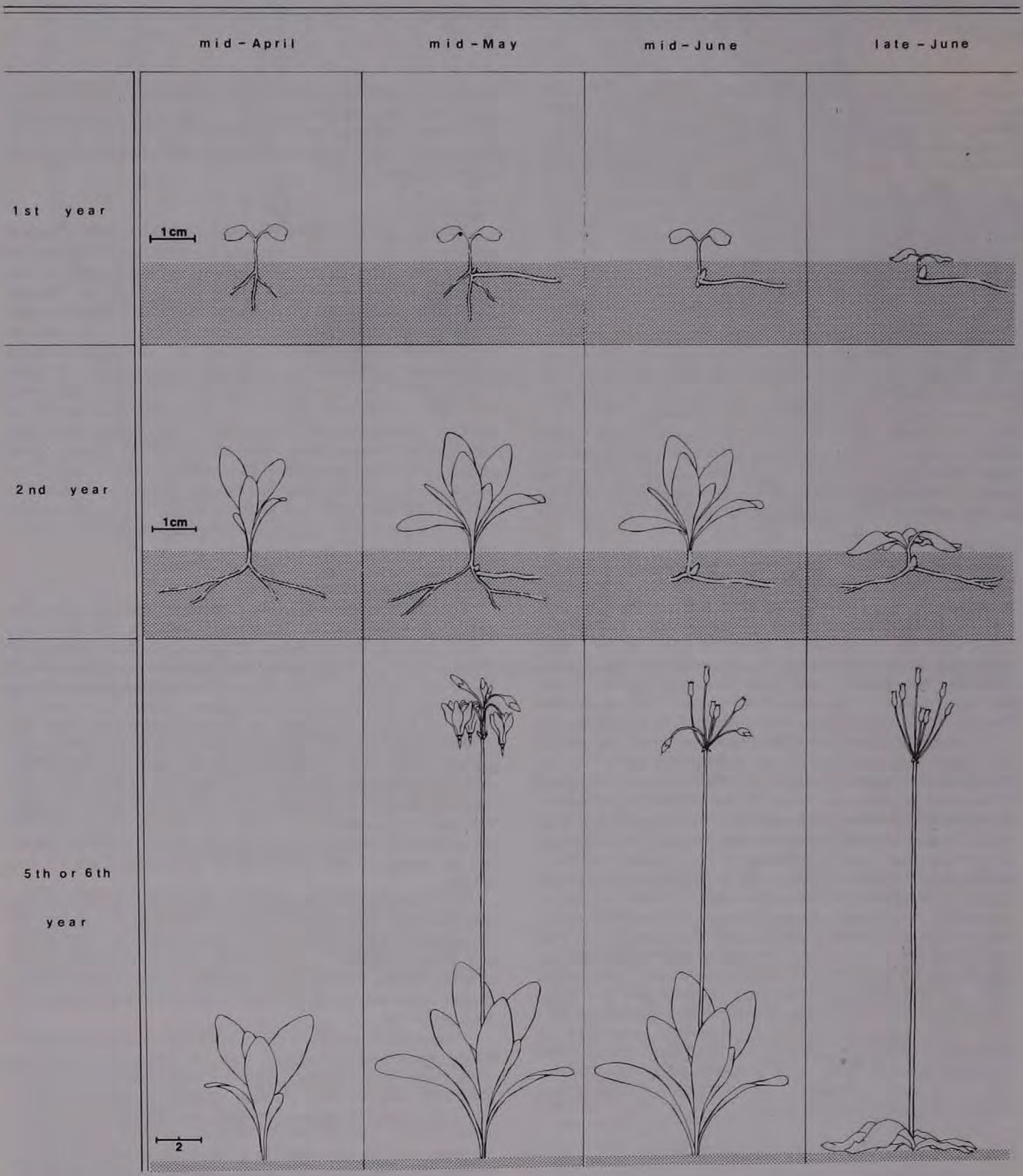

Figure 1. The life cycle of Shooting Star. Note that after a brief period of growth in the spring of the year, the leaves wither, leaving behind only the oversummering and wintering subterranean bud with a fleshy root attached.

second year, but they do not indicate whether the observation period extended beyond a third season. As I have intimated, one will doubtlessly observe considerable variation in the length of the maturation period as a function of local environmental conditions.

Propagation of Mature Plants

The most reliable method for increasing the number of flowering plants, whether in a garden or in a prairie restoration, is the simple division of what I call the "root-crown" system (Figures 2 and 3). A mature plant that has reached maturity and remained in place for a number of years will have developed a dense clump of interconnected buds and fleshy roots that can be divided into as many individuals as there are buds. My experience suggests the best time for this is in late summer, about the end of July or early August, after all of the developing capsules have ripened and one can gather the seeds for further sowing. An essential exercise when replanting the buds with a few of their fleshy roots attached involves copious watering to reestablish the soil capillarity. Failing this, the newly placed underground parts are subject to drying and frost heaving. Even with watering, the transplants benefit greatly from adding a substantial layer of mulch.

Under outdoor garden conditions, where individual plants lack competition for space, one can expect at least one, large, new bud to form each growing season. This allows further division of a root-crown system to take place rather soon. The root crown-system shown in Figure 2 has resulted from about six years of growth, starting with a single bud. I have not observed whether more than one bud can develop in a single season.

Use of Giberrellins to Accelerate Maturation

Seedlings in the coytledon stage can be made to bypass the normal dormant period (from July to March) by advancing their development to the juvenile leaf stage, the equivalent of their second year's growth (Figure 1), with the application of GA at a concentration of 500 ppm in an aqueous spray. I have found the most satisfactory product to be Pro-Gibb marketed by Abbott Laboratories. It comes in an alcoholic concentrate of 3.91%. Adding 12.78 ml of the concentrate to 1.0 liter of water yields a 500 ppm solution that should be stored at cold temperatures and used within one month. A drop of surfactant, such as Kodak Foto-flo or even ordinary dishwashing liquid detergent, added to a liter of the 500 ppm solution will reduce surface tension on the leaves of the plants when sprayed with the GA. Application of the GA to the cotyledons should take place as soon as they have reached full expansion. The sprayed plants should be removed from sunlight or from a bright greenhouse for a few hours to allow absorption of the hormone. The procedure has not been totally satisfactory. About half of the plants respond as expected. Circumventing the normal first dormant period following the cotyledon stage is the chief benefit to be derived from this method. The action of the hormone is to induce continuous growth and thereby invest the seedling with a greater chance of survival when placed outdoors.

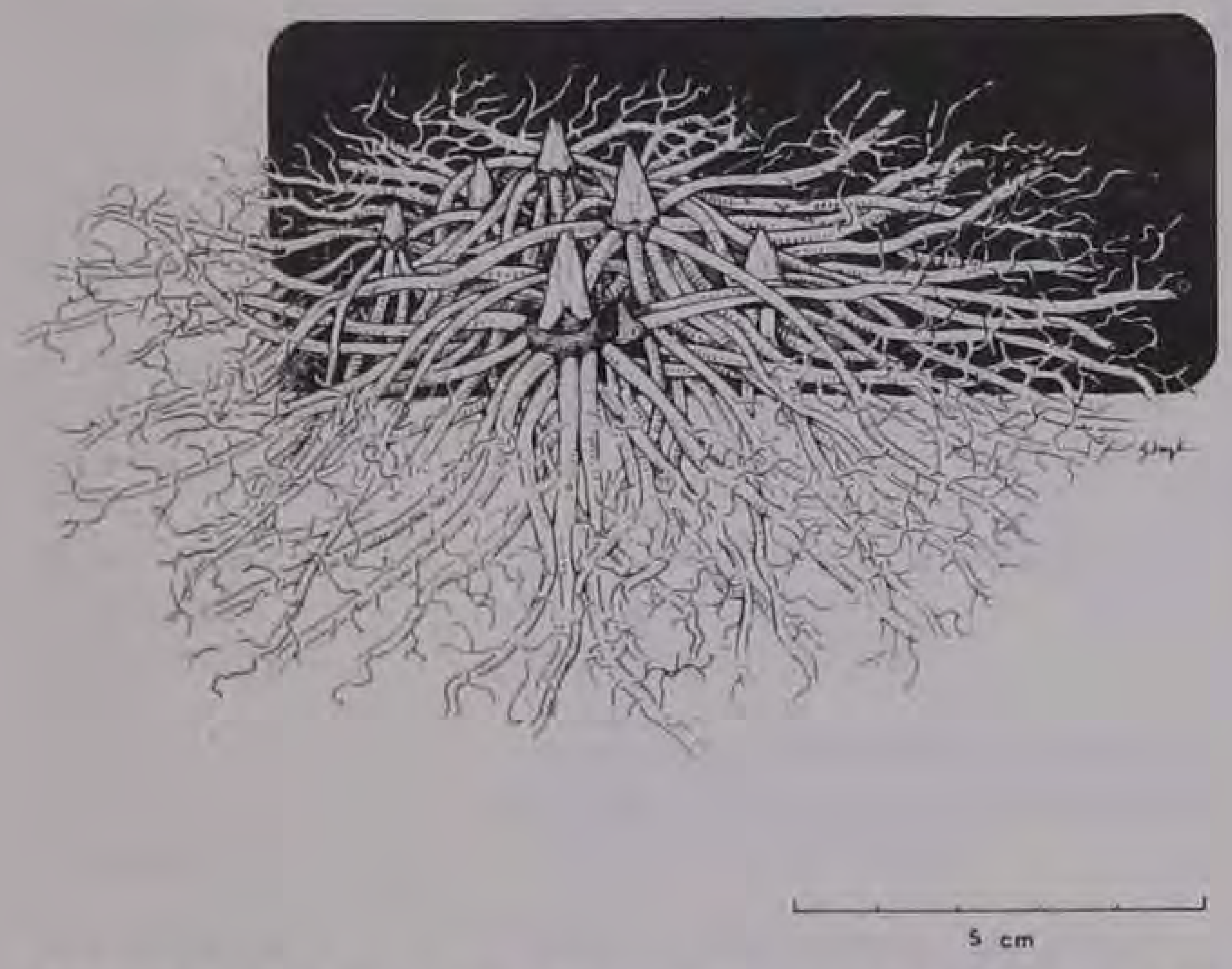

Figure 2. An intact "root-crown" system lifted in late July from an outdoor garden location. See also Figure 3.

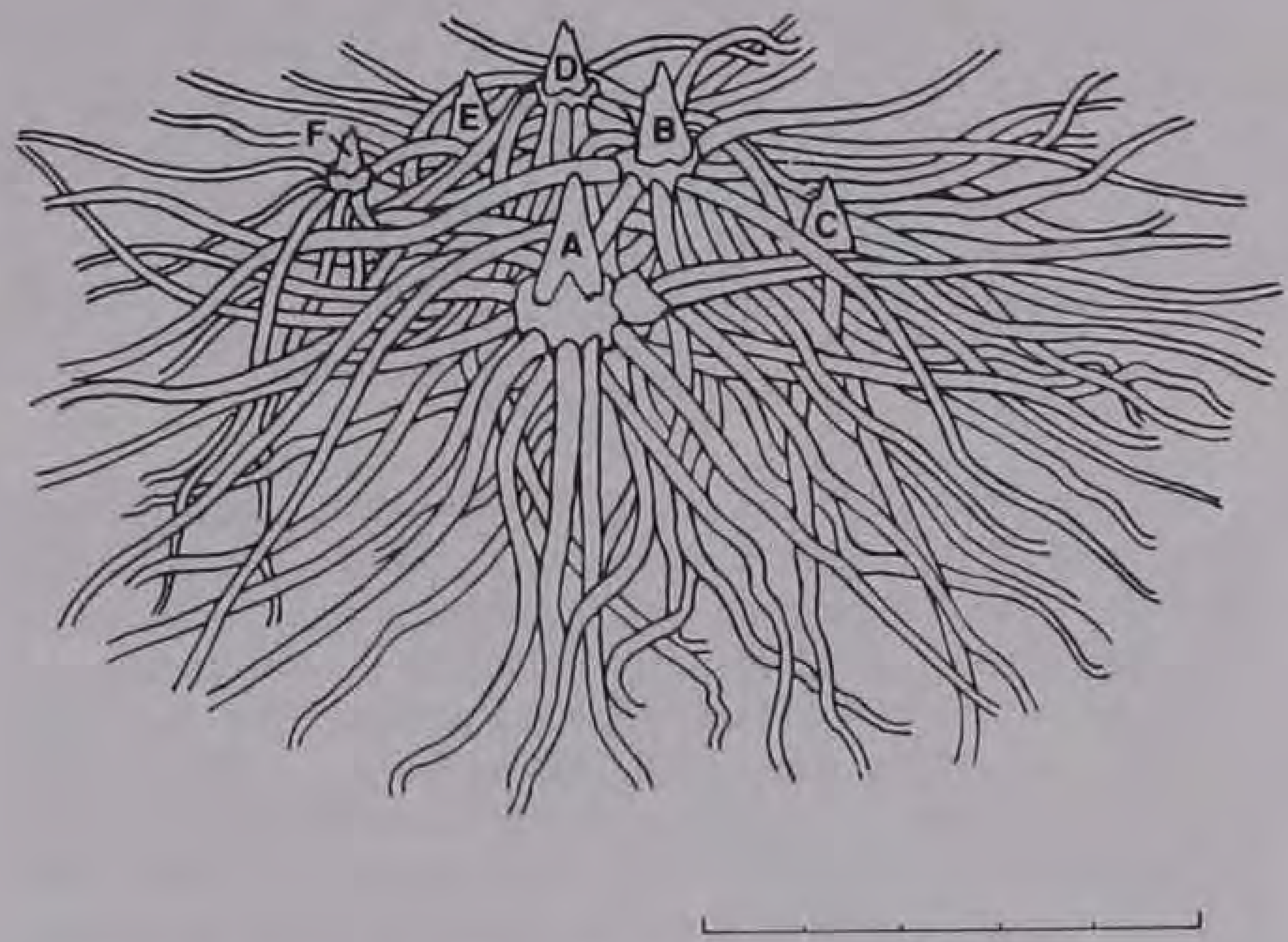

Figure 3. Tracing of the root-crown system pictured in Figure 2 without the tender rootlets and with the buds (crowns) labeled in descending order of size. Separating each of the buds from the network permits vegetative propagation. Under garden conditions, at least one new bud is added to the root-crown annually.

Continuous illumination with artifical lighting over a period of not less than 30 days following the full development of the cotyledons has, in one instance, produced the same results as the application of GA; that is, the young plants began to produce juvenile leaves without first passing through the dormant period. Attempts to repeat this, which was a consequence of a serendipitous malfunction in the lighting timer of a growth chamber, have not been successful. Experiments are underway to try again.

Propagation of Mature Plants with Gibberellins

Success in the use of GA on seedlings led to the question of whether mature plants could be treated in the same way. Root-crown systems of a single genotype (numbered 9096A-H below), more or less identical to that shown in Figure 3, were lifted on 26 July 1990, cleaned, separated into eight individual buds with attached fleshy roots, numbered, and submerged in varying concentrations and durations of GA as follows:

9096 A & B - 100 ppm GA, 2 hours

9096 C & D - 100 ppm GA, 12 hours

9096 E & F - 500 ppm GA, 2 hours

9096 G & H - 500 ppm GA, 12 hours.

Potting in a mixture of Pro-Mix, loam, and sand (4:1:1) took place immediately after the GA treatment. The pots were then placed in a greenhouse with normal daylight. Developing leaves were visible by 31 July on 9096 E and 9096 F, and by 6 August, buds in all eight pots had begun to sprout. Owing to the inability to prevent excessively high temperatures in the greenhouse, the pots northeastern Kansas; data for *A. ovalifolia* were obtained from populations in southern and central Wisconsin. For *A. perennis* and *A. variegata*, populations from southern Illinois and southeastern Missouri were used for the data collection. In addition, a few isolated plants of *A. meadii* from northeastern, central, and southern Illinois and a single plant of *A. ovalifolia* from northeastern Illinois were also used. While most of the data were obtained from wild populations, for 16 of the species, data were also taken from dozens of specimens grown from seed. The two species not grown were *A. stenophila* and *A. viridis*.

Although much of the data collected from year to year were from known individual plants and populations, new plants and populations were continually sought in order to diversify the population samples. The new individuals and populations, especially for the less common species, were found by searching natural communities where they could be expected to occur. Assistance in locating such areas was provided by knowledgeable local field ecologists and botanists. Other site information was obtained from herbarium specimens found at the Field Museum of Natural History, Chicago, and the Morton Arboretum, Lisle, Illinois. Fortuitous discoveries of individual plants or populations were made from time to time.

Some milkweeds typically produced a single flowering stem (genet) from the rootstock, while others produced multiple flowering stems (ramets). *Asclepias meadii* is an example of a species which usually produced only one flowering stem. On the other hand, rootstocks of *A. tuberosa* usually produced multiple flowering stems. In fact, a specimen of *A. tuberosa* which had been grown from seed, produced a bushy plant of 33 flowering stems (Betz, unpublished data). *Asclepias syriaca* and *A. verticillata* commonly produced large rhizomatous clones of flowering stems that extended over large areas and contained hundreds of stems. Because of this variability in stem production found among the 18 species, the unit of observation used for collecting data was the individual stem.

To ensure that plants were visited at the proper time for observation of flowering and subsequent ripening of pods, a chart was constructed for the 18 species studied. Data for this chart were obtained primarily from field studies, but these were supplemented by data obtained from herbarium specimens at the Field Museum of Natural History, Chicago, and the Morton Arboretum, Lisle, Illinois.

Collection of data for most species was done by counting without damaging the plant part under observation. For certain species, determination of the number of flowers per stem was comparatively easy and thus could be carried out in the field. However, some of the more common, weedier species, such as A. syriaca, had so many flowers per umbel that field counting was not feasible. Instead, umbels were removed and taken separately in marked plastic bags into the laboratory for counting. If flowers had already fallen from an umbel, it was still possible to get an accurate count by observing scars left on the peduncle.

A similar difficulty held for *A. hirtella*, *A. stenophila*, and *A. verticillata*, in that they produced large numbers of lateral umbels. These species frequently had lost most or all of the flowers on the lower umbels of a stem and at the same time embryonic flowers were developing in the uppermost umbels. Such stems were cut at the base and carried into the laboratory for thorough study and counting. Frequently, a magnifying glass was required to count the tiny embryonic flowers in the uppermost umbels.

For other species, counting flowers per stem was sometimes difficult and time consuming. In *A. incarnata*, a stem typically produced so many flowers and umbels that a direct count of the flowers per stem was almost impossible. Because of this, a second method was developed: The mean number of flowers per umbel was multiplied by the mean number of umbels per stem to produce a mean number of flowers per stem. Comparing the results obtained by this method with those obtained by counting, showed that both methods were essentially equivalent (Table 4). For example, in *A. purpurascens*, the calculated mean number of flowers per stem was 73.0. Using the direct count method, the number was

Table 2. Flowers per umbel in Asclepias.

Species	*Range*	*Mean (S.D.)*[a]	*n*[b]
A. amplexicaulis	1-50	24.6 (9.5)	171
A. exaltata	1-44	13.6 (6.3)	216
A. hirtella	14-101	47.0 (18.8)	168
A. incarnata	11-51	28.2 (8.2)	154
A. lanuginosa	1-63	22.9 (9.2)	87
A. meadii	1-26	12.0 (3.3)	643
A. ovalifolia	1-25	9.3 (3.3)	237
A. perennis	1-38	14.1 (5.1)	115
A. purpurscens	1-75	30.4 (13.5)	292
A. quadrifolia	1-35	15.6 (6.3)	232
A. stenophila	3-29	17.0 (6.0)	86
A. sullivantii	1-40	29.2 (5.7)	223
A. syriaca	31-186	83.6 (27.7)	309
A. tuberosa	1-37	11.9 (4.9)	665
A. variegata	9 - 52	30.2 (10.0)	45
A. verticillata	3-25	11.7 (1.7)	453
A. viridiflora	18-108	50.5 (18.5)	133
A. viridis	1-23	7.2 (3.3)	246
Total			4,475

[a] S.D. = standard deviation.
[b] n = sample size.

Table 3. Umbels per stem in *Asclepias*.

Species	*Range*	*Mean (S.D.)*[a]	*n*[b]
A. amplexicaulis	1	1.0 (-)	171
A. exaltata	1-7	2.6 (1.4)	111
A. hirtella	1-27	8.7 (4.6)	450
A. incarnata	1-195	35.2 (35.5)	266
A. lanuginosa	1	1.0 (-)	87
A. meadii	1	1.0 (-)	643
A. ovalifolia	1-4	1.7 (1.8)	186
A. perennis	1-6	3.1 (1.5)	73
A. purpurascens	1-7	2.4 (1.1)	168
A. quadrifolia	1-4	1.7 (0.6)	103
A. stenophila	4-15	9.3 (2.5)	18
A. sullivantii	1-5	2.1 (0.8)	268
A. syriaca	1-9	4.3 (1.8)	319
A. tuberosa	1-25	7.4 (4.9)	458
A. variegata	1-5	2.3 (1.0)	19
A. verticillata	1-36	9.1 (7.1)	101
A. viridiflora	1-5	2.2 (1.0)	143
A. viridis	1-8	3.7 (1.6)	100
Total			3,714

[a] S.D. = standard deviation.
[b] n = sample size.

66.7. For *A. sullivantii*, the comparative figures were 40.3 and 41.9, and for *A. verticillata*, these figures were 106.5 and 105.8.

This second method was also used in calculating mean numbers of seeds per stem. This was done by multiplying the mean number of seeds per pod by the mean number of pods per stem.

Also determined were the number of pods per stem, the number of seeds per pod, and thus the number of seeds per stem. If possible, recently ripened pods were used in counting seeds because it was more difficult to separate seeds from the comma in the dry state.

RESULTS

Flowers per Umbel

Counts were made of the number of flowers within individual umbels for all 18 species of milkweed (Table 2). This involved a total of 4,475 umbels. Ranges of flower numbers per umbel and mean number of flowers per umbel were determined for all species. The number of flowers per umbel ranged from 1 to 186. *Asclepias viridis* had the lowest mean number of flowers per umbel (7.2), while the highest mean number of flowers per umbel was exhibited by *A. syriaca* (83.6). For most milkweed species, the number of flowers per umbel gave normal distribution curves. However, there was a tendency for the curve to skew slightly toward the higher number of flowers.

Umbels per Stem

Umbels were counted for 3,714 stems of the 18 species to determine the number of umbels produced per stem (Table 3). *Asclepias incarnata* had the widest range in number of umbels per stem (1-195) and also produced the highest mean number of umbels per stem (35.2). In contrast, three species (*A. amplexicaulis*, *A. lanuginosa*, and *A. meadii*) produced only one umbel per stem. For most milkweed species, the number of umbels per stem gave normal distribution curves. Similar to the curves obtained for the flowers per umbel, there was a slight tendency for the curves of number of umbels per stem to skew toward the higher number of umbels. This was very pronounced for *A. incarnata*, which produced the most strongly skewed curve of all the species studied. While 77% of the stems in this species produced between 1 and 50 umbels, 23% of the stems produced 51 to 195 umbels.

Table 4. Flowers per stem in *Asclepias*.

Species	*Range*	*Mean (S.D.)*[a]	*n*[b]	*Mean**
A. amplexicaulis	1-50	24.6 (9.5)	171	24.6
A. exaltata	2-119	38.6 (26.8)	76	35.4
A. hirtella	197-631	369.4 (150.7)	10	408.9
A. incarnata	— - —	— —	—	992.6
A. lanuginosa	1-63	22.9 (9.2)	87	22.9
A. meadii	1-26	12.0 (3.3)	643	12.0
A. ovalifolia	2-39	15.8 (7.7)	109	15.8
A. perennis	12-112	42.8 (28.5)	33	43.7
A. purpurascens	3-195	66.7 (41.4)	85	73.0
A. quadrifolia	5-67	26.9 (13.8)	103	26.5
A. stenophila	— - —	— —	—	158.1
A. sullivantii	9 - 101	41.9 (19.2)	99	40.3
A. syriaca	200-858	474.7 (173.4)	33	359.5
A. tuberosa	7-226	89.5 (69.5)	61	88.1
A. variegata	9-143	70.3 (39.0)	19	69.5
A. verticillata	23-379	105.8 (88.9)	53	106.5
A. viridiflora	20-283	77.5 (55.5)	23	111.1
A. viridis	5-55	26.4 (12.1)	67	26.6
Total				1,672

[a] S.D.= standard deaviation.

[b] n = sample size.

* Calculated mean (numbers of flowers per umbel X numbers of umbels per stem).

Flowers per Stem

The mean number of flowers per stem was determined for 1,672 stems for 16 of the 18 species of milkweeds. This determination was made by direct counting and by calculating mean number of flowers per umbel multiplied by the mean number of umbels per stem (Table 4). Results obtained using the two methods were generally the same. For example, *A. quadrifolia* had a mean number of flowers per stem of 26.9 by direct counting and a mean of 26.5 by calculation. *Asclepias meadii* yielded the smallest mean number of flowers per stem (12.0). *Asclepias incarnata*, however, produced the highest mean number of flowers per stem (992.6), as determined by the indirect methods of calculation only.

For *A. syriaca*, there was a notable difference in the mean number of flowers per stem obtained by the method of direct counting (474.7) in contrast to that obtained by the method of calculation (359.5). This is probably due, in part, to the population sample used for the direct count being too small (33); also, partially due to the fact that the direct count involved only a few clones with limited diversity. The mean number of flowers per umbel determined for the small sample of 33 stems by count (84.7) was approximately the same as that determined for the larger more diverse population by calculation (83.6). However, there was a difference found in the mean numbers of umbels per stem, using the two methods. The counted population had a mean number of 5.6 umbels per stem in contrast to the mean number of 4.3 umbels per stem calculated for the other population. The counted sample had on average 1.3 more umbels per stem, and thus each stem had a theoretical capacity of 110.1 more flowers per stem. The actual number obtained by counting was 115.2. Thus, the discrepancy shown between the mean number of flowers per stem, when comparing the results obtained from direct counting (474.7) with the results obtained from calculating (359.5), can be explained by the larger mean number of umbels per stem in the relatively small population sample used for direct counting. Lesser differences in the mean number of flowers per stem observed in two other species (*A. hirtella* and *A. viridiflora*) also seem to be due to the small samples used in the direct count (Table 4).

Pods and Pods per Stem

Marked variation in pod production also occurred for the 18 species studied. The number of pods produced on 4,794 stems observed ranged from 0 (1) to 75 (Table 5). The high of 75 was found for *A. incarnata*. The mean number of pods per stem varied from a low of 0.005 in *A. lanuginosa* to a high of 16.1 in *A. incarnata*.

Milkweed flowers possess two separate ovaries, each with the potential to produce a mature pod. These twin pods share the same pedicel. In one study of *A. syriaca*, 5.4% of the pods were double or twins (Sparrow and Pearson 1948), and in another study on the same species, the percentages ranged from 9.5 to 24.5% (Moore 1947). In the present study, 3.7% of the pods produced by *A. syriaca* were twin or double pods. The figure for *A. amplexicaulis* was 0.83%; for *A. sullvantii*, 2.3%; and for *A. verticillata*, 1.9%.

Milkweed pods (follicles) varied greatly in size, shape, and the manner of attachment of pedicels to the peduncle (Table 6.). In general, the larger, coarser milkweeds, such as, *A. amplexicaulis*, *A. purpurascens*, *A. sullivantii*, *A. syriaca*, and *A. viridis* had the largest pods, and the smaller less robust species, such as *A. quadrifolia* and *A. lanuginosa*, had the smallest ones. *Asclepias meadii* had long,

Table 5. Pods per stem in *Asclepias*.

Species	*Range*	*Mean*	*n*[a]
A. amplexicaulis	0-5	1.3	136
A. exaltata	0-6	0.7	73
A. hirtella	0-15	2.9	387
A. incarnata	0-75	16.1	184
A. lanuginosa	0-1	0.005	437
A. meadii	0-2	0.06	643
A. ovalifolia	0-3	0.15	71
A. perennis	0-2	1.4	5
A. purpurascens	0-5	1.2	46
A. quadrifolia	0-2	0.06	103
A. stenophila	0-1	0.18	11
A. sullivantii	0-5	1.5	329
A. syriaca	0-42	4.6	645
A. tuberosa	0-9	1.8	671
A. variegata	0-1	0.24	17
A. verticillata	0-20	2.6	931
A. viridiflora	0-8	2.0	55
A. viridis	0-5	1.9	50
Total			4,794

[a] n = sample size.

Table 6. Size of pods in Asclepias

Species	*Length (cm) (Range)*	*Length (cm) (mean)*	*Diameter (cm) (mean)*	*n*[a]
A. amplexicaulis	8.3 - 15.5	12.6	1.9	86
A. exaltata	7.8 - 12.8	10.5	1.2	128
A. hirtella	7.0 - 11.8	9.8	1.5	167
A. incarnata	5.9 - 8.5	7.4	0.8	54
A. lanuginosa	— - —	7.6	1.2	1
A. meadii	6.9 - 15.8	11.8	1.1	40
A. ovalifolia	4.8 - 6.6	6.4	1.8	11
A. perennis	3.9 - 6.8	5.6	1.0	16
A. purpurascens	9.0 - 15.0	11.8	1.4	59
A. quadrifolia	8.8 - 10.4	9.6	0.5	12
A. stenophila	9.2 - 10.1	9.6	0.7	2
A. sullivantii	8.2 - 13.6	10.4	2.3	150
A. syriaca	6.5 - 13.6	10.0	2.9	112
A. tuberosa	8.4 - 15.5	11.8	1.3	151
A. variegata	10.5 - 15.7	12.7	1.0	3
A. verticillata	4.7 - 10.2	7.2	0.5	160
A. viridiflora	6.5 - 14.5	9.6	1.5	103
A. viridis	— - —	—	—	—
Total				1,255

[a] n = sample size.

narrow pods, while *A. perennis* had short, globular ones. Three species (*A. incarnata*, *A. quadrifolia*, and *A. verticillata*) had erect pods on erect pedicels. *Asclepias perennis* had pendulous pods (hanging down) on recurved or slightly deflexed pedicels. All of the other 14 species of A*sclepias* had erect pods on deflexed pedicels.

Seeds and Seeds per Pod

A total of 127,220 seeds were counted in 1,672 pods for the 18 species of *Asclepias* studied (Table 7). The numbers of seeds per pod ranged from a low of 11 in *A. meadii* to a high of 309 in *A. syriaca*. The mean number of seeds per pod varied from a low of 22.7 in *A. ovalifolia* to a high of 244.3 in *A. syriaca*. The larger, coarser species of milkweeds produced the highest mean number of seeds per pod. These were *A. amplexicaulis* (117.8), *A. purpurascens* (180.7), *A. sullivantii* (182.2), and *A. syriaca* (244.3). On the other hand, the smaller, less robust species usually had the smallest pods with the lowest mean number of seeds in them. These were *A. lanuginosa* (39.0) and *A. quadrifolia* (27.6). A few species produced pods with inflated endocarps; these pods were moderately large, but contained relatively few seeds. Two such species were *A. hirtella* (51.2) and *A. ovalifolia* (22.7).

While the seeds of all *Asclepias* species are similar, there were some morphological differences among them. For example, the seeds of *A. sullivantii* were larger and lighter brown than seeds of *A. syriaca*. *Asclepias hirtella* produced seeds which had larger margins and had a darker brown color than most of the other milkweed species. The seeds of *A. lanuginosa* were smaller and darker than many of the other species. *Asclepias perennis* seeds do not bear a tuft of silky hairs (coma) at the hilum like all of the other species.

A variable number of seeds for the species studied appeared to lack embryos and/or sufficient amounts of food reserves for normal germination (0.2 to 4.8%). Species that had higher percentages of these apparently undeveloped seeds were *A. meadii* (14.0%), *A. lanuginosa* (60.1%), and *A. ovalifolia* (78.0%). Two species, *A. ovalifolia* and *A. quadrifolia*, produced one pod each that was normal in size but contained only visibily undeveloped seeds. Two other species, *A. lanuginosa* and *A. meadii*, produced one pod each that was of normal size but completely empty and without any seeds.

Seeds per Stem

The mean seeds per stem for the 18 species were obtained by multiplying the mean number of seeds per pod by the mean number of pods per stem. *A. lanuginosa* produced the lowest mean number of seeds per stem (0.2), while *A. syriaca* had the highest (1,123.8). The mean seeds per stem for the other 16 species of *Asclepias* were as follows: *A. amplexicaulis* (153.1), *A. exaltata* (59.6), *A. hirtella* (148.5), *A. incarnata* (872.2), *A. meadii* (3.6), *A. ovalifolia* (3.4), *A. perennis* (58.1), *A. purpurascens* (216.8), *A. quadrifolia* (1.7), *A. stenophila* (8.0), *A. sullivantii* (273.3), *A. tuberosa* (132.8), *A. variegata* (25.9), *A. verticillata* (118.8), *A. viridiflora* (170.8), and *A. viridis* (209.6).

DISCUSSION

For most milkweeds, all the flowers in a given umbel open within a day or two of each other (Betz, unpublished data). These are thus capable of being pollinated for a period of about five or six days (Morse 1987, Betz, unpublished data). In order for pollination to be effective, the pollinating insect, usually a hymenopteran (Betz, unpublished data), must insert the pollinia into the stigmatic chamber of the flower with the convex side of the pollinia entering first. Within a few days following pollination, the pedicels of the flowers that have been successfully pollinated will begin to thicken and, in most species, deflex downward, followed by the development of a small pod.

Transfer of a pollinium into a stigmatic chamber of a flower does not necessarily mean that a pod will form. If the pollinium is

Table 7. Seeds per pod in *Asclepias*.

Species	*Range*	*Mean (S.D.)*[a]	*n*[b]
A. amplexicaulis	60-186	117.8 (20.4)	86
A. exaltata	24-121	84.1 (18.9)	128
A. hirtella	31-70	51.2 (7.2)	197
A. incarnata	16-113	54.2 (14.1)	189
A. lanuginosa	38-40	39.0 (1.0)	2
A. meadii	11-112	59.6 (22.9)	45
A. ovalifolia	15-37	22.7 (8.9)	6
A. perennis	26-51	41.5 (6.3)	22
A. purpurascens	91-245	180.7 (31.5)	59
A. quadrifolia	19-33	27.6 (4.4)	14
A. stenophila	40-49	44.5 (5.0)	2
A. sullivantii	116-253	182.2 (24.8)	148
A. syriaca	164-309	244.3 (31.2)	182
A. tuberosa	47-92	73.8 (14.7)	151
A. variegata	88-116	108.0 (14.0)	4
A. verticillata	17-66	45.7 (9.5)	297
A. viridiflora	20-129	85.4 (19.3)	130
A. viridis	85-154	110.3 (24.8)	10
Total			1,672

[a] S.D. = standard deviation.
[b] *n* = sample size.

inserted in reverse into the stigmatic chamber, the pollen may germinate, but the pollen tube may never reach the ovary to fertilize the ovules (Galil and Zeroni 1969). In other instances, pods may be initiated, but will abort because the flower has been pollinated with a pollinium from the same or genetically closely related plant (Sparrow and Pearson 1948, Kephart 1981). A pod may also abort due to competition among the developing pods for limited nutrients from the parent plant. Eleven plants of *A. meadii*, grown from seed in pots and flowering in their third year of growth, were placed in a virgin prairie (Markham Prairie, Markham, Illinois) to be pollinated by resident bumble bees. Within one week 21 pedicels began to enlarge and twist downward, indicating that pollinia had been inserted into stigmatic chambers and that pods were beginning to form. Eventually most of these initiated pods fell off, leaving only three pods to mature. Pod abortion has been reported by others (Sparrow and Pearson 1948, Wilson and Price 1974).

Abortion of developing pods was also observed for a potted plant of *A. meadii* grown from seed which had been hand-pollinated with pollinia taken from an isolated non-seed setting plant of *A. meadii* from southern Illinois. This plant initiated two pods which eventually became unequal in size. For a time both pods grew at the same rate, and it appeared that both would mature. However, one began to outgrow the other. Gradually, the smaller one stopped growing, began to decrease in size, regressed, and finally degenerated into a tiny vestigal appendage adjacent to the mature pod. It appeared that the larger pod was using nutrients derived from the smaller one.

In their floral development, milkweeds have evolved two different strategies. The first strategy, exhibited by *A. amplexicaulis*, *A. lanuginosa*, and *A. meadii*, involves the production of a terminal umbel with all flowers opening within a day or two of one another. The species showing this strategy appear to rely on one or two dependable pollinators (Betz 1989). The second strategy, exhibited by the species, *A. hirtella*, *A. incarnata*, *A. stenophila*, and *A. syriaca*, involves the successive production of a number of umbels having flowers in bloom over a longer period of time. Individual plants of *A. hirtella* have been observed to have ripened pods, open and shedding seeds at the base of the plant, while at the upper end of the stem, umbels with flowers were being visited by various pollinators. The milkweed species exhibiting this strategy have a larger number of different insects to pollinate their flowers as compared to the first group (Betz, unpublished data). Because of possible unfavorable pollinating conditions during a short blooming period—inclement weather, etc.—species with a terminal umbel would be less likely to produce a pod than would the second group of species with a succession of blooming umbels.

The range and mean number of flowers and umbels per stem produced by most milkweeds today are undoubtedly the same as in presettlement times. However, it is possible and highly probable that the numbers of pods per stem produced by some milkweed species today are less than those which would have been produced in presettlement times. It is difficult to conceive that *A. meadii* and *A. quadrifolia*, both with a mean pod per stem ratio of 0.06, and *A. lanuginosa*, with a ratio of 0.005, could have sustained adequate populations over long periods of time in the presettlement prairies and savannas with such low pod production (Table 5). There is also the possibility that in presettlement times, as today, the number of pods produced per stem varied in an irregular manner about a mean. When large populations are considered over relatively extended periods, mean number of pods per stem may have been related to the mean number of umbels per stem that a species produced. For four species, this relationship may have further involved the production of a mean number of about one pod per umbel for their populations generally. This is suggested by the following data: *A. amplexicaulis* produced a mean of 1.3 pods per umbel, *A. syriaca* had 1.1, *A. viridiflora* (0.9), and *A. sullivantii* (0.7). This relationship did not appear to hold for the other 14 species of milkweeds under present day conditions. However, in the past with higher populations of both milkweeds and pollinators this relationship may have existed.

Further, it should be noted that in presettlement times there were large expanses of prairies, savannas, open and closed forests, marshes, and intervening ecotones. These plant communities in turn supported high populations of insect species, including the pollinators of the various milkweeds. This helped to assure an ample supply of seeds (and seedlings) to maintain adequate population levels necessary for survival.

The ecological communities of today are much altered. They are fragmented and degraded, and there is heavy competition from non-native plants. Populations for all insects, including the pollinators of milkweeds, are probably low in number, in part, due to the lack of suitable habitats and food sources and to the widespread use of insectides. While there is little experimental evidence to document this decrease in insect populations, there is some historical evidence. During the 1930s, when lower speeds were prevalent, the radiators, windshields, and bumpers of automobilies had to be cleaned of hundreds of insects killed after driving only a few miles through the countryside (Betz, personal observation). Again during the 1930s, hundreds of thousands of monarch butterflies (*Danaus plexippus* L.) passed through the inner city of Chicago each fall on their migrations southward (Betz, personal observation). These observations of insect abundance are things of the past. Insect populations may have been even greater during presettlement times.

The weedy species *A. syriaca* is apparently maintaining adequate population levels today, just as it did in presettlement times. In part, this is the result of the availability of large areas of disturbed ground as well as the production of relatively large numbers of flowers, pods, and seeds. Moreover, the formation of large clones, sometimes containing hundreds of flowering stems, has also helped. The success of this species in maintaining adequate populations may also be due, in part, to the fact that their flowers are pollinated by a higher proportion of exotic species, including the Eurasian honey bee (*Apis mellifer* L.) (Betz, unpublished data).

On the other hand, many of the other milkweed species are undergoing population declines because of the degradation and fragmentation of their habitats and the consequent loss of their insect pollinators. It would appear that many milkweeds, especially the smaller ones with narrower ecological tolerances and few flowers and seeds per stem, may have difficulty in surviving under present ecological conditions. A few species, such as *A. meadii*, *A. lanuginosa*, and *A. ovalifolia*, are now included on threatened or endangered species lists.

Finally, many of the milkweed populations observed for this study over the past 30 years have disappeared, and few new populations have appeared to take their place (Betz, personal observation). Thus, this study would be difficult to replicate today.

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ILLINOIS BUNDLEFLOWER: PROSPECTS FOR A PERENNIAL SEED CROP

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Abstract. Illinois bundleflower (*Desmanthus illinoensis* (Michx.) MacM., Fabaceae) is a warm-season perennial legume of the North American grasslands. It is rated by some as our most important native legume. Illinois bundleflower seeds contain 38% protein on a dry weight basis. In this review of The Land Institute's research in developing Illinois bundleflower as a perennial seed crop, we present the species' characteristics, nutritional value, nitrogen fixation capability, and potential for genetic improvement.

INTRODUCTION

An examination of agriculture reveals practices that use nature not as a model, but as a mine. Soil erosion, reduction of biological diversity, groundwater contamination, salinization, and dependence on fossil fuels are some results of this extractive approach. The Land Institute is a research and education organization devoted to a sustainable agriculture, that uses nature as its model. To solve the problems in agriculture, we recognize the problem of agriculture: its inherent disruptiveness. To lessen the negative effects of agriculture, we try to mimic the patterns and processes of the prairie ecosystem native to central Kansas. Each year, Land Institute research staff and interns study the prairie and conduct experiments in plant breeding with the aim of developing an agriculture that is a mixture, or polyculture, of seed-producing perennials.

This paper reviews The Land Institute's research in developing Illinois bundleflower, *Desmanthus illinoensis* (Michx.) MacM., as a perennial seed crop, examining the species' nutritional value, nitrogen fixation capability, and potential for genetic improvement. Illinois bundleflower has been called our most important native legume (Great Plains Flora Association 1986), yet there are no published reports of genetic variability within this species. We have been studying Illinois bundleflower at The Land Institute since 1979. Although it has not historically been a human food, preliminary data on nutritional value, seed yield, genetic variability, and nitrogen fixation suggest that it has promise as a perennial grain legume.

DISCUSSION

Characteristics

Illinois bundleflower is a self-fertile, perennial legume of the North American grasslands. It is found north to Minnesota, west to Colorado, and south from Texas to Florida. Native stands occur in prairies, rocky open ground, wooded slopes, stream banks, roadsides, and railroad rights-of-way (Latting 1961). It is readily eaten by livestock and has been included in range revegetation programs (Great Plains Flora Association 1986).

Unlike many prairie perennials, Illinois bundleflower sets seed its first year of growth. Seeded in May, it flowers by mid-July and matures by early September. Germination is greatly enhanced by seed scarification.

Although Illinois bundleflower has relatively high yields for a perennial, mature seed pods readily open and drop their seeds, or shatter. In 1988, The Land Institute's plant breeder, Peter Kulakow, noticed three naturally-occurring crosses between a normal shattering collection and a non-shattering collection from Knoxville, Tennessee. The hybrids showed intermediate shattering characteristics, increased vigor, and different bundle shapes (Epp 1989). Much of our Illinois bundleflower breeding work now centers around these non-shattering hybrids.

In our research to develop a "domesticated prairie" we are seeking answers to some basic biological questions. Because a large part of a perennial plant's energy goes into its roots, whereas in an annual most energy goes to seed production, are perennialism and high seed yield mutually exclusive (Jackson 1980)? Long-term studies at The Land Institute have shown Illinois bundleflower yields to be highest the first year of growth, and to subsequently decline. To date, however, these studies are of no-input monocultures. We are conducting similar long-term-yield studies in bicultures, growing Illinois bundleflower with a warm-season, perennial bunchgrass, eastern gamagrass (*Tripsacum dactyloides* (L.) L.), to study overyielding (Foreman 1989).

Nutritional Value

Because we are interested in Illinois bundleflower as a food crop, we began our investigations by sending plant clippings and seed to the U.S. Department of Agriculture Poisonous Plants Research Laboratory in Logan, Utah, to test for oxalates, cyanides, nitrates, and alkaloids. No toxic levels were found (Bruns 1985).

The seed of Illinois bundleflower is high is protein: 38% on a dry weight basis (Table 1). For comparison, soybeans are 40% protein. To test for protein digestibility, we sent cooked and uncooked seed to the University of Nebraska's Food Protein Research Group. Protein from uncooked seed was 69% digestible; protein from seed boiled for 60 minutes was 83% digestible. (Kulakow et al. 1990). An estimate of the degree to which protein is utilized in the human body is called the computed Protein Efficiency Ratio (c-PER); Illinois bundleflower's c-PER is close to that of cooked oats, at 1.8 (Table 2). Its seed is high in sulfur-containing amino acids, which is unusual in vegetable proteins (Bruns 1985).

Nitrogen Fixation

A second question we are exploring is whether a perennial polyculture can maintain itself through nitrogen fixation and solar energy, as the prairie ecosystem does, and thus reduce the need for fertilizer. The percentage of nitrogen derived from symbiosis in a perennial legume such as Illinois bundleflower is likely to be greater than that of annual grain legumes, as the root nodules are perennial and fixation may begin earlier in the season (Salisbury

Table 1. Proximate analysis of Illinois bundleflower seed on a dry basis (data from Kulakow et al. 1990).

	Collection	
Nutrient	*415*	*391*
	-------%-------	
Crude protein	38.9	36.7
Carbohydrate	33.3	35.5
Crude fat	0.3	0.8
Fiber, ADF[1]	22.9	21.0
Ash	4.6	6.0

Undried seed contained 11% moisture.

[1] ADF = Acid digestible fiber.

Table 2. Computed Protein Efficiency Ratio (c-PER) of Illinois bundleflower seed protein and other food proteins.

Protein source	*c-PER*
Uncooked Illinois bundleflower	1.4
Illinois bundleflower, boiled 30 min	1.6
Illinois bundleflower, boiled 60 min	1.8
Hard red winter wheat	1.2
Whole corn	1.2
Oats, cooked	1.8
Soybeans, cooked	2.3
Casein (milk protein)	2.5

Data from Kulakow et al. 1990.

and Ross 1985). It has been shown that nitrogen transfer occurs in mixed swards (Brophy 1987); thus, we hope to use Illinois bundleflower as both a seed-bearing and a soil-building component of an agriculture that mimics the prairie.

In 1988, we tested the nitrogen fixation of 37 Illinois bundleflower collections from different geographic locations. We grew seedlings inoculated with rhizobia in a perlite-vermiculite mix in our greenhouse and fertilized with a nil-nitrogen micronutrient solution every thirty days. At seventy days, the seedlings were assayed for acetylene reduction. Roots or whole plants were sealed in containers and exposed to acetylene. After one hour, a gas sample was withdrawn and injected into a gas chromatograph to measure ethylene production. We found that nitrogen fixation rates of Illinois bundleflower are comparable to those of soybeans and alfalfa. Variation in fixation rates in the 37 collections tested is adequate to select for high nitrogen fixation lines in our breeding program (Benson and Vail 1988).

Breeding Program

In 1978, we planted Illinois bundleflower in our herbary, as part of a living inventory of 300 perennial species. In 1982, we chose to study Illinois bundleflower in greater detail because of its vigor and high seed yield. In subsequent years, we conducted germination, pollination, planting density, and yield trials. In 1987, we expanded our germ-plasm studies and, in 1988, established a large Illinois bundleflower germ-plasm evaluation plot to study variation in vigor, yield, plant morphology, and shatter resistance. Plants were grown from seeds collected from 82 counties in ten states. Seeds were scarified, inoculated with rhizobia (obtained from the Nitragin Company, Milwaukee, Wisconsin), and planted in the greenhouse in March. Seedlings were transplanted to the field in May and June (Benson and Vail 1988). Yields in this study ranged from 615 to 1700 kg/ha with a mean yield of 1200 kg/ha. This is comparable to yields of soybeans in this region (Benson and Vail 1988). From this study, we have chosen twenty high-yielding collections to advance in our work with Illinois bundleflower. We are also evaluating new germ plasm collections.

We are continuing to observe the non-shattering hybrids found in 1988, and recent plantings of seeds from these hybrids have shown great variation in growth habit, seed shattering, bundle shape, stem color, and seed size. The variation in seed size seems to indicate that the non-shattering trait may be useful in breeding for both shatter-resistance and larger seeds.

CONCLUSIONS

Illinois bundleflower plays an important role in The Land Institute's research in sustainable agriculture that uses nature—the prairie—as its model. Although specific end uses for this species still need to be identified, preliminary agronomic and nutritional analyses are encouraging. First year yields for Illinois bundleflower, a perennial, are comparable to those of soybeans in this region. The answer to our first question, are perennialism and high seed yield mutually exclusive, may be *no*. Illinois bundleflower also fixes appreciable amounts of nitrogen. We hope to use Illinois bundleflower as a seed-bearing fertilizer, grown in a polyculture of perennial grain crops.

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SILPHIUM PERFOLIATUM (CUP-PLANT) AS A NEW FORAGE

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Abstract. Cup-plant, *Silphium perfoliatum* L., is native only to prairies of the eastern parts of North America. It was introduced to Europe and western USSR around 1750; since then it has been prized there as a showy, long-flowering, horticultural perennial. Around 1957, it was noticed to show potential as a productive low-maintenance fodder crop for ensiling for livestock feeding. In 1972, Sokolov and Gritsak published, in English in *World Crops*, a summary of their 15 years findings. Since then more than 100 papers have been published from eleven countries—but none from the United States. This paper summarizes those reports, supplemented by personal observations. Field trials have now begun here. It is a long-lived perennial herb; its high productivity, ease of husbandry, high protein content, good feed value for meat and milk production, and good palatability rival alfalfa; these qualities make it worthy of study in its home country.

INTRODUCTION

Protagonists for scholarly study of the fast-vanishing tropical rainforests emphasise the potential for pharmaceutical, biological, or commercial values of as-yet unrecognised constituent species. American Indian lore suggests that prairie plants may hold comparable promise.

This paper briefly reviews and summarises the extensive work that has been done at many overseas centers over several decades on cup-plant (*Silphium perfoliatum* L.) which, although endemic to our all-but vanished North American prairie, has not been studied previously in the United States as a fodder.

METHODS

This literature review is culled mainly from papers that have been abstracted in two English-language journals: Biological Abstracts (Biosis, 2100 Arch St, Philadelphia, PA 19103) and C.A.B International Abstracts (845 North Park Avenue, Tucson, Arizona, United States 85719). The majority of the original papers abstracted there are written in Cyrrilic script or in Japanese ideograms, and full copies are not generally available in libraries in the United States. When those papers that I have obtained contain summaries in English or in French I have used those also. Many of the papers cover only the first two or three years of a field study, and so cannot give valid information about the characteristics of a plant that does not achieve full production and quality until after the fourth year after seeding. I have supplemented this paper, especially in the historical section, from books in the libraries of Kew Gardens, London, England, and of the Herbarium at the Southern Methodist University, Dallas, Texas. In addition to the agronomic papers reviewed here, Biological Abstracts records another 15 papers of biochemical or pharmaceutical studies on the constituent chemicals of the plant. If you want the citations for those papers, please let me know.

My most important references, each covering many years work, are from copies of full-length papers: Professors Sokolov and Gritsac published in English in 1972 a review of their fifteen years fieldwork. Professor Kawahara, who worked on cup-plant for over a decade before he retired, sent to me from Japan six of his papers in Japanese; they have summaries in English, and some of his tables and illustrations are captioned in English. Dr Niqueux started his field-work in 1974; he published his results in French in 1981. I went to France in 1990 to talk with him, but he had retired, and could not be traced. This literature review continues; I will gladly send a full, updated list of over 130 references on request.

This paper is further supplemented by my observations made in 1990 on a 40 x 40 ft trial plot in Arkansas, United States, and on another plot 10 x 20 ft in Arlington, Texas, United States; both of these areas have acid sandy soil (cup-plant does not thrive on the highly alkaline soils of Dallas).

Table 1. Countries that have published reports, listed in order of first publication.

Russia	33	1972
Ukraine	6	1973
Lithuania	6	1973
Japan	12	1976
France	2	1978
China	?	1980?
G.D.R.	2	1982
Switzerland	1	1982
Bulgaria	3	1984
New Zealand	1	1987
Chile	1	1987

Table 1 lists published reports by country and date of first publication. This list is certainly incomplete. For example, one author numbered his sequential reports as far as 22, yet only 6 of them appear in the Abstracts. Again, others have not been abstracted: for example, China is reported as having supplied seed to New Zealand, but no abstracts appear from China. There are no abstracts from the United States or from Canada.

HISTORY

Origin

All species in the genus *Silphium* in the tribe Heliantheae (family Asteraceae) occur natively only in eastern North America. Cup-plant is today found in the wild sporadically from southern Canada to northern Arkansas, in open prairie clearings in bottomland woods.

Horticulture

The most recent comprehensive review (Puia and Szabo 1985) revealed that the early reports on its cultivation mention cup-plant only as an ornamental. It was listed in the inventories of central European gardens as early as 1830, but Puia and Szabo (1985) could find no reference about when, where, or by whom it was first introduced from North America.

Linnaeus (1759) named it. The earliest mention in European gardens that I have found is in 1762, in a taxonomic listing of the holdings of the Montpelier Gardens in France (Gouan 1762). The Royal Botanic Gardens in England (`Kew Gardens') record it as introduced to them by Peter Collinson in 1766 (Aiton 1789). In the United States, the first horticultural record is from 1860 (Sokolov and Gritsak 1972).

Agriculture

The published literature suggests that around 1950 the USSR planned a nationwide search for innovative and alternative winter forage crops—but I have not found this inference stated explicitly. The first publication in English about cup-plant as a fodder and silage crop was made by Sokolov and Gritsak (1972), who started to evaluate it in 1957 and continued the investigation for many years, working from the Feed Resources Laboratory of the Chernovits State University in Russia. Vavilov and Kondratev (1975) reviewed some 50 candidate novel and traditional species that had been investigated for high-yield silage fodder; 10 promising species were selected for further study. Part one of the *Proceedings of the All-Union Conference on Technology of Cultivation of New Fodder Crops* was published in Russian only (Saratov-Engels 1978); the performance of some 30 species was reported. The finalists in this search were *S. perfoliatum* and *Heracleum sosnovskyi*, which is native to the USSR. Many other foreign centers around the world have started trials on cup-plant since then, but I have no information on which are presently active.

CHARACTERISTICS

Habitat

Cup-plant is a perennial herb of the northeastern United States and southeastern Canada; it grows in moist sandy bottomlands and floodplains, near streambeds, in or adjacent to open woodland.

Genetics

It assimilates atmospheric CO_2 through the Type C_3 pathway; the chromosome count is haploid 7 (R.Fisher, personal communication Bowling Green University, Ohio, U.S.A.).

Climatics

The winter-dormant roots can survive freezing to -30 C, and they can survive flooding for 10-15 days (Niqueux 1981, Koshkin 1975). The plant needs full sun for optimal growth and can withstand high summer heat provided it has enough water. Best growing temperatures are around 20 C.

Year One

Germination.

Cup-plant germinates in the spring from seeds which have cold-stratified in the soil. Germination is not photo-dependent and does not need fluctuating temperatures (Kawahara et al. 1977a). During the first year, the seedling forms a long deep taproot, nourished by 12-14 leaves in the form of a rosette; the leaves measure up to 75 cm long and are chordate-triangular in shape (Kawahara et al. 1976). After midsummer, several buds begin to form underground at the base below the leaves and are fully formed by first frost; then the summer leaves wither and die. A small winter rosette of several leaves may now form.

Year Two

Basal leaves.

In the spring of the second year, as the soil warms, the winter leaves, if any, die, and one or more of the dormant buds develop broad chordate-triangular alternate leaves up to 30-35 cm long. At first they are nourished from the reserves in the thickened base of the seedling's taproot.

Roots.

As the new leaves develop, adventitious roots arise from the base of the bud, which is now seen to be a compressed rhizome; these roots originate from the axillae of its scale-leaves. These roots are 30-150 cm long, and 1.5-2 mm diameter for most of their length. Some grow down, others spread radially under the soil surface; they do not branch (Stanford, personal observations 1990).

Flowering stem.

After midsummer, when roots are well established and the rosette has 12-15 alternate leaves (Sokolov and Gritsak 1972), a single flowering stem develops from the apex of each large rhizome. This stem at maturity is 1-3 cm wide, 2-4 m high, and bears up to 17 leaves (Niqueux 1981); it is remarkably square and sharp-cornered in section, hence a colloquial name for this plant: square-weed. From the fourth or fifth node upwards, the leaves become opposite. After first frost, the flowering stems die back to the ground.

Stem leaves.

About 8-14 pairs of opposite leaves form at intervals along the stem (Niqueux 1981); these can attain 30 cm in length and 20 cm in width. Because their petioles are widely winged, each leaf seems to be triangular, with its base at the stem; each base is fused with that of the other in its pair, forming a cup which the stem appears to pierce (connate-perfoliate); hence the alternative colloquial name: cupweed.

Branches.

The stem terminates in a single flower-bud. While this is developing, each leaf of the upper cupped pair produces one sidestem from its node. These side-stems each terminate in a flower-bud and have a pair of opposite leaves half-way up their stem. Each of these pairs of secondary leaves subtend a similar flowering stem, and this symmetrical branching process repeats itself 4-6 times over a period of 6-10 weeks, until first frost stops further growth.

Flowers.

Each flower looks superficially to be of the typical sunflower type, with a central disc and two ranks of ray florets. But, as is the distinguishing feature of all silphia, these disc florets are atypical in that although structurally they appear to be bisexual, only the stamens are fertile. The ray florets are female only (Barkley 1986). Seeds are produced through cross-fertilisation with insect pollinators. Each flowerhead produces 20-30 seeds (Niqueux 1981).

Seeds.

Each seed is 9-15 mm long, 6-9 mm wide, strongly flattened, with a maximum thickness of 1 mm; 1,000 seeds weigh about 23 gm (Niqueux 1981).

Year Three and Beyond

Spread.

The pattern of multiple budding at the base of each mature flowering stem is repeated annually. Strong competition by the leaves of the largest buds quickly shades out those of the smaller ones, which abort, but many buds (rhizomes) remain dormant. During the next winter, the above-ground central core of each now-dead stem rots away, but the underground periphery that bears the next year's buds persists for several years, as a woody storage organ. After four to seven years, the growing centers are so far from the original taproot that it ceases function and rots away.

Longevity.

The multi-rhizomed clone from a single seed has been observed to persist in this way for over 15 years; roots are known from botanical gardens which are probably more than 50 years old (Niqueux 1981).

Stem density.

Each seed gives rise to five to seven stems in the second year and to

Table 2. Cup-plant harvest compared to alfalfa (t/ha), modified from Sokolov and Gritsak (1972)

Crop and method of sowing	*Harvest as-cut* (WW)	*Yield*	
		Dry matter	*Protein*
Cup-plant, 70 cm row spacing	11.38	1.926	0.29
Blue Alfalfa, 15cm rowspacing	5.6	0.995	0.21

over 50 by the fifth to seventh year; they stabilize at a density of 38-40 flowering stems/m^2 (Niqueux 1981, Puia and Szabo 1985).

AGRICULTURE

Biotype

It is remarkable that all these reports originate from seed that went to central Europe a century or two ago. The New Zealand trial (Douglas et al. 1987) used seed sent from China, which in its turn probably came from the early central European accessions.

Soil

Cup-plant prefers good rich sandy bottomland, which perhaps is flooded some years and is risky for conventional winter row-crops. A good soil-moisture throughout the summer is essential for large yields, and even for survival (Vavilov et al. 1974).

Establishing from Seed

In the spring, after the the previous winter's rowcrop has been harvested, the soil should be tilled. Emergent weed seedlings should be killed with commecial Treflan at 7-8 kg/ha (Filatov et al. 1986) or 2-4 kg/ha of active compound (Vavilov et al. 1978). Cleaned, pre-chilled seed is then applied at 10-40 kg/ha at 40-70 cm spacing.

The first year's growth is not strong: to control weeds, inter-row harrowing must be done three to four times, or paraquat applied (Niqueux 1981); in-row weeds must be hoed or pulled by hand. In the second year, harrowing may be needed early in the season, while the leaves of the crop are emerging (Vavilov et al. 1978).

Establishing from Roots

Alternatively, for small trials and for breeding selection, the entire root system can be dug up while dormant. The large root cluster should be divided into sections, each containing at least one large and several smaller buds. They should be planted with the crowns just below soil surface. There is no need to dig deeply to plant the old roots, for they are mainly storage organs to feed the growing crown; they will cease function before the soil heats up, while the first few leaves feed the rapidly growing new roots (Stanford, personal observation).

HARVESTING

Seed

When starting a new trial from only a small, seed sample, the usual first objective is to multiply the seed stock. While the extended flowering season is splendid for bees, it also makes seed harvesting difficult since the seeds shatter almost as soon as ripe, even while new flowerhead production is continuing. Repeated hand collecting over the season can produce a high seed yield, but machine collection must be timed to secure the best return from a single annual cut. The first four orders of blooming yield the highest seed production: 100-250 kg/ha (Sokolov and Gritsak 1972). If the stems have been left standing, they should be cut and chopped or shredded immediately after the first hard frost; this disposes of the standing trash and mulches the rhizomes.

Silage

For silage, a higher total biomass dry-weight (DW) yield, richer in protein, is gained by double-harvesting: the first harvest is in the summer just as the first flowerbuds start to open; the second harvest should be as the flowerbuds of the second flush begin to open seven to nine weeks later. The dry weight (DW) is 13-16% of the as-cut wet-weight (WW) (Niqueux 1981).

Harvest Composition

The leaves have 15-20% DW, the stem 12-15% DW; this averages 14.3% DW at first harvest. At second harvest, the figures are >18%, >17%, and 17.5%, respectively (Niqueux 1981).

Yield

The first year's yield is poor, but it increases quickly in subsequent years. By the fourth or fifth year, the as-cut yield of the two harvests combined is about 80-120 t/ha/yr under good moisture and fertilization regimens (Filatov et al. 1986). This should continue for many years, because although the root is perennial, each successive crop is annual and so has youthful vigor. Analyses of average yields are given in Tables 2, 3 and 4.

Table 3. Essential amino-acids content of the dry weight from Sokolov and Gritsac (1972).

Vegetative stage of plants	*Date of sampling*	*Height of plants, cm*	*Percent-age of leaves*	*Part of plant*	*Protein as % of dry matter*	*Content of amino acids as % of total protein*							
						Argi-nine	*Valine-methio-nine*	*Histi-dine*	*Leucine*	*Lysine*	*Threo-nine-glutamic acid*	*Tryp-to-phan*	*Phenyl-alanine*
Before budding	Apr 10	76	69	leaves	24.47	3.06	7.35	3.39	4.69	5.39	9.72	0.98	8.70
				stalks	14.28	1.68	3.99	2.24	3.71	2.10	8.68	0.37	3.78
Start of budding	Jun 25	193	56	leaves	20.10	3.23	8.50	3.12	5.22	7.76	6.27	9.85	7.51
				stalks	9.15	3.28	2.29	4.59	2.51	3.93	2.40	0.34	2.18
Budding	Jul 10	207	50	leaves	19.65	3.15	6.61	4.47	4.83	4.07	3.05	0.46	6.16
				stalks	7.85	2.55	3.95	4.71	2.55	5.73	2.16	0.38	2.29
Start of budding of aftercrop plants	Sep 1	95	44	leaves	16.38	7.32	10.87	1.22	9.40	6.41	11.72	0.61	7.33
				stalks	4.65	4.30	3.87	4.73	1.94	2.58	2.79	0.97	5.59
Budding of aftercrop plants	Oct 15	102	43	leaves	14.17	5.79	8.98	4.09	8.35	5.91	14.63	0.92	8.20
				stalks	3.83	4.38	4.64	2.06	3.61	2.81	5.41	0.90	7.22

Table 4. Chemical composition of compass-plant compared with other fodder plants, expressed as % of dry matter, from Sokolov and Gritsak (1972).

Plant	*Parts of plant*	*Dry matter*	*Proteins*	*Albumin*	*Fat*	*Cellulose*	*Nitrogen-free extracts*	*Ash*	*Calcium*	*Phos-phorus*
Silphium — before budding, May 10	leaves	14.8	24.5	22.0	3.5	11.8	46.8	13.4	1.72	0.57
	stalks	7.6	14.3	10.8	2.7	19.7	50.4	12.9	0.93	0.62
Silphium — budding, July 10	leaves	21.5	19.7	16.3	3.5	15.0	48.8	13.0	3.06	0.41
	stalks	17.9	7.9	4.9	2.4	35.1	47.4	7.2	1.54	0.36
Silphium — before budding of aftercrop, Aug. 15	leaves	13.2	26.2	22.3	3.3	13.0	49.6	7.9	2.16	0.52
	stalks	9.9	8.2	5.2	1.7	29.0	50.8	10.3	1.72	0.45
Silphium — budding of aftercrop, Oct. 15	leaves	21.5	14.2	11.8	3.2	14.3	48.5	19.8	3.33	0.47
	stalks	22.8	5.9	3.9	1.5	32.2	41.6	18.8	1.55	0.43
Blue alfalfa — start of flowering	leaves	25.4	22.8	15.1	4.5	16.3	40.6	15.8	2.85	0.26
	stalks	24.3	11.2	6.5	1.6	36.8	41.7	8.7	1.24	0.27
Maize — waxy ripeness	whole plant	33.2	8.7	5.0	2.3	20.9	61.8	6.3	1.20	0.20
Red clover — start of flowering	whole plant	21.8	16.7	13.2	2.6	31.4	40.8	8.5	1.88	0.23

Fertilizing

Such high annual productivity places a great demand on the soil nutrient reserves. Each season some 250-300 kg of N, 75-100 kg of P_2O_5, and 500-750 kg of K_2O are exported; this must be replaced to maintain productivity (Niqueux 1981).

Ensiling

Silage made from as-cut WW biomass is high in butyric acid and low in lactic acid, with a pH of 5.2. Several authors report that as-cut ensiling gives too wet a mash, and they warn that the runoff liquors contain a lot of the nutrients (Maslinkov and Donev 1987; Nedwaras and Marchulenis 1987) and should be retained.

Enrichment

Some authors recommend that formic acid be added at the rate of 3.5-5 litres/WW ton (Niqueux 1981, Puia and Szabo 1985); others recommend that the freshly harvested biomass be wilted or partially hayed before ensiling. When prewilted from 85-80% WW moisture down to 70%, the butyric acid in the silage falls to 0.03%, and lactic acid rises to 1.93%, with an overall pH of 5.5. This makes a good feed (Kawahara et al. 1977b). Alternatively, a dry forage can be mixed in: wood pulp (Niqueux 1981), grains (Sokolov and Gritsak 1972), or grain chaffs (Niqueux 1981).

Silage Quality

Quality of cup-plant silage compares well with maize silage (Niqueux 1981) (Tables 2 and 3).

Grazing

Livestock must not be allowed to open-graze the growing crop: their hooves would do too much damage to the newly-forming underground buds that will provide next year's crop. Niqueux (1981) reports that sheep will eat fresh-cut plants. Puia and Szabo (1985) report that cattle will not do so, but I have watched cattle freely eating it in the field. A middle-aged lady told me that the tender young leaves newly emerging in the spring make a good culinary vegetable, either as fresh salad or cooked; her mother frequently served them thus when she was a child.

Pests and Diseases

Cup-plant is generally disease-free. In summertime, the stems are sometimes attacked by Sclerotinia. In cool damp autumns, some flowerbuds wilt and turn black before opening, attacked by Botrytis (Niqueux 1981). Puia and Szabo (1985) reported that some of their seedlings' roots were eaten by a ground-dwelling beetle (`courtilier').

Honey Production

The long blossoming season and the profusion of flowering heads under seed-production management provide a rich source of honey; 150 kg/ha/yr is mentioned (Sokolov & Gritsak 1972).

Other Products

The Silphium genus provides a number of compounds in their saps, some of which have pharmaceutical properties. Cup-plant for example contains silphiocide A—a triterpene glycoside (Davidyants et al. 1984), substances having nematocidal properties (Gommers 1973), and extracts that hasten burn-wound healing in rats (Kuyantseva and Davidyants 1988).The summary presented here is a condensation of a longer paper which contains over 100 references and many more tables. If you would like to receive that, please write to me for a copy.

ACKNOWLEDGEMENTS

I am grateful for continuous assistance in libraries and in the field from Bess Woodard; for historical assistance from Barny Lipscomb, Curator of the Herbarium at the Southern Methodist University, Dallas; and for assistance in my fieldwork from Aaron and Joyce Cawley.

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A FIELD EVALUATION OF NATIVE MINT FAMILY PLANTS AS HONEY BEE FORAGE IN IOWA[1]

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Abstract. A preliminary field plot was established in 1986 to assess the suitability of various species of native, perennial mint family plants (Lamiaceae) as food plants to support honey bees (*Apis mellifera* L.). This report summarizes honey bee preference data collected over three growing seasons, along with general information on these plants' range of adaptation and ease of culture. In general, *Agastache* populations had the highest levels of honey bee visitation, followed by populations of *Pycnanthemum*. Honey bee activity on populations of *Monarda* and *Salvia* was much less. Within *Agastache* and *Pycnanthemum* species, bee preference differed greatly among plant populations. The most promising populations of *Agastache* and *Pycnanthemum* from the preliminary field plot are now being evaluated in a replicated trial.

INTRODUCTION

In 1986, a field plot was established at the North Central Regional Plant Introduction Station (NCRPIS) in Ames, Iowa to evaluate the suitability of native mint family plants as sources of nectar for honey bees. Earlier publications (Widrlechner 1987, 1988) describe the rationale for planting for this purpose and contain detailed information on how plant populations were initially selected and established in the test plot.

This report summarizes data collected during 1987, 1988, and 1989 on honey bee visitation and on the ability of these plants to thrive under field conditions at Ames, Iowa.

MATERIALS AND METHODS

Populations of anise hyssop (*Agastache foeniculum* (Pursh) Kuntze), catnip giant hyssop (*Agastache nepetoides* (L.) Kuntze), Korean-mint (*Agastache rugosa* (Fisch. & Meyer) Kuntze), bee balm (*Monarda fistulosa* L.), horsemint (*Monarda punctata* L.), pilose mountain mint (*Pycnanthemum pilosum* Nuttall), slender-leaved mountain mint (*Pycnanthemum tenuifolium* Schrad.), Virginia mountain mint (*Pycnanthemum virginianum* (L.) Durand & Jackson), and Pitcher's sage (*Salvia azurea* Lam. var. *grandiflora* Benth.) were established in a 0.16 ha field at the NCRPIS during 1986 to 1988. The test plot design is a completely randomized design with most populations being represented, at least initially, by 49 or more plants. It is described in detail by Widrlechner (1987).

Beginning the year after planting, counts of the numbers of honey bees visiting each population were taken when the plants were flowering (mid-June to mid-September). Honey bees were counted by three trained workers chosen for count accuracy and repeatability. Counts were performed only under the following conditions (Senechal 1990):

1. Air temperature between 24 C and 34 C;
2. Average wind velocity below 2.25 m per sec;
3. No impending storms.

Air temperatures below 24 C are associated with decreased bee activity (Burrill and Dietz 1981, Szabo 1980). On windy days, the workers found it difficult to distinguish individual honey bees among the moving plants. Shortly before the arrival of summer thunderstorms, bee activity appeared to decrease suddenly as bees returned to their hives.

In each year of this study, there were six evaluation periods, each approximately two weeks long. For every evaluation period, the workers counted all honey bees in the test plot six times, three times during mornings and three times during afternoons to average any difference in attractiveness owing to time of day. Ayers et al. (1987) reported that honey bee visits to some plants were greatly influenced by time of day. At certain times of year, however, the weather did not permit six counts to be made in a two-week period. In such cases, the period was lengthened until the six counts could be made. The average period was 15 days, but ranged from 12 to 23 days.

For every population evaluated, a mean bee count was calculated for each period. A bee visitation index (BVI) was then calculated to determine relative bee preference using the formula:

$$\frac{\sum_{i=1}^{6} [(\text{mean bee count}_i) \times \#\text{ of days in period}_i]}{\#\text{ of live plants.}}$$

Live plants were counted each spring to allow standardization of bee-count data and to determine the plants' persistence and ability to overwinter.

Although BVI values quantify the cumulative use of these plants by honey bees during the growing season, differences in BVI values are influenced by a large number of factors such as duration of flowering, number of flowers per plant, amount of nectar per flower, and competition with other insects. Except for duration of flowering, no data were systematically collected in this test on factors influencing bee preference.

BVI values for given species were statistically analyzed in rank form by using a Rank-Sum Multiple Comparison Test (Dunn 1964). This test was chosen because of small sample sizes and extreme heterogeneity of variances.

RESULTS AND DISCUSSION

General Observations

The years 1987, 1988, and 1989 presented three very different test conditions. 1987 was particularly wet with intermittent flooding of the test plot. More than 700 mm of rain fell between 1 May and 1 October 1987. 1988 was one of the hottest and most difficult summers at the NCRPIS in recent memory. Temperatures exceeded 40 C five times, and only 408 mm of rain fell between 1 May and 1 October 1988. In 1989, even less rain fell during the growing season (377 mm), but the rain was more evenly distributed, and temperatures were more moderate.

During the test period, the number of honey bees kept at the NCRPIS increased substantially. In 1987, 340 nucleus hives were used for the controlled pollination of germplasm collections at the NCRPIS. This increased to 465 nucleus hives in 1988 and 761 in

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[1] Journal Paper No. J-14232 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa. Project No. 1018

Table 1. Honey bee preference for species evaluated.

Species evaluated	*Year*	*Bee visitation index*		*N*[1]
		Mean	*Range*	
Anise hyssop	1987	115.34 c[2]	87.4-145.1	5
	1988	117.16 c	95.5-156.4	8
	1989	168.95 c	33.7-241.8	11
Korean-mint and hybrids[3]	1987	120.8 abc	108.4-133.2	2
	1988	193.75 c	101.2-287.1	4
	1989	487.45 c	53.9-1110.5	4
Catnip giant hyssop	1987	80.7 abc		1
	1988	40.1 abc		1
	1989	152.17 bc	122.3-194.3	3
Bee balm	1987	0.58 ab	0.0-2.3	16
	1988	0.48 a	0.0-1.3	20
	1989	3.45 a	0.3-16.2	20
Horsemint	1987	5.2 abc		1
	1988	14.0 abc		1
	1989	62.4 abc		1
Pilose mountain mint	1988	58.9 abc		1
	1989	210.1 bc	185.5-234.7	2
Slender-leaved mountain mint	1987	16.27 bc	7.6-30.2	6
	1988	20.83 bc	7.9-35.5	7
	1989	105.33 bc	46.2-183.1	8
Virginia mountain mint	1987	36.3 bc	21.1-67.5	4
	1988	23.42 bc	9.9-52.5	5
	1989	137.1 c	99.3-185.0	6
Pitcher's sage	1987	0.04 a	0.0-0.2	12
	1988	4.55 ab	0.0-8.7	12
	1989	6.13 ab	2.1-15.6	12

[1] Number of populations evaluated.

[2] Mean separation within year by using Rank-Sum Multiple Comparison Test, $P \leq .3$.

[3] Hybrids between Korean-mint and anise hyssop replaced Korean-mint during 1988 and 1989 (see text).

1989. The number of bees visiting the test plot rose at a somewhat higher rate, nearly doubling from 1987 to 1988 and doubling again from 1988 to 1989.

Summaries of the results of bee counts are given in Tables 1, 2, and 3. Table 1 shows the BVI for each plant species tested. Table 2 lists the specific populations with the highest BVI in each year. Table 3 summarizes seasonal differences in flowering and honey bee visitation for each species. The following sections describe results by genus in more detail.

Giant Hyssop

Three species of giant hyssop were planted in the test plot: anise hyssop, catnip giant hyssop, and Korean-mint. The first two species are native to the United States and Canada, and Korean-mint is native to Asia (Lint and Eppling 1945). When the test plot was established, evaluations were to be performed on species native to the north-central United States, but samples of Korean-mint were obtained inadvertently as anise hyssop. Both these species are aromatic and have flowers of similar colors, but Korean-mint has rugose, dark green leaves with cordate bases, whereas anise hyssop has shiny, bright green leaves with feltlike undersides and cuneate bases (Lint and Eppling 1945). Evidently these species are occasionally confused in some botanical gardens and in the seed trade.

Korean-mint plants are especially susceptible to verticillium wilt (Block et al. 1989) and did not persist well in the test plot. However, they reseeded heavily, and many of the seedlings outperformed the maternal parents. Senechal (1990) used gel electrophoresis and essential oil analyses to identify interspecific hybrids between Korean-mint and anise hyssop in the test plot. These hybrids are more vigorous than Korean-mint and have generally replaced Korean-mint in the test plot. The hybrids are also sterile (Vogelmann 1985) and flower over a longer period than Korean-mint.

Tables 1, 2, and 3 show that these hybrids are among the most attractive populations tested for honey bees. These plants are being propagated vegetatively from stem cuttings for a replicated trial.

Anise hyssop is well adapted to Iowa field conditions. Some populations were among the top lines each year (Table 2), with a population from Barnes County, North Dakota among the best of all populations each year. Anise hyssop has been used commercially as a source of nectar for honey production in Washington (Mayer et al. 1982), and the results reported here show that selected populations of this species may also be useful for this purpose in Iowa.

Catnip giant hyssop performs well when conditions are not too hot and dry, but its flowering period is less than 45 days, while the flowering period was usually more than 80 days for anise hyssop and Korean-mint (Table 3).

Bee Balm

Although *Monarda fistulosa* is known as bee balm, this is apparently not because of its attractiveness to honey bees (Table 1). Many species of bumble bees (*Bombus* spp.) and butterflies (Lepidoptera) collected its nectar, but honey bees cannot compete for nectar from such long corolla tubes in the presence of these other insects. Bee balm was also extremely susceptible to powdery mildew (*Erisyphe cichoracearum* DC) (Giles et al. 1980, Hayward 1983), which weakened the plants. Horsemint was visited by the honey bees more often than was bee balm (Table 1), but these plants were dominated by digger wasps (Sphecidae) and were not long-lived (Widrlechner 1987).

Mountain Mint

Three species of mountain mint were evaluated. In general, the plants survived well, showing few problems with adaptation or disease. However, the hot, dry weather of 1988 reduced flowering and bee activity dramatically in populations of Virginia mountain mint. In nature, this species tends to be found on more mesic sites than the other two species evaluated, slender-leaved mountain mint and pilose mountain mint.

Populations of slender-leaved mountain mint and Virginia mountain mint vary greatly in attractiveness to honey bees (Table 1). Only in 1989 were the best populations of these two species as attractive as an average population of anise hyssop.

For pilose mountain mint, the situation is more encouraging. Pilose mountain mint performed better than the other mountain mints in 1988 and 1989 (Table 1). It is attractive to honey bees for longer than the other mountain mints. Its flowering period lasted more than 60 days, while slender-leaved and Virginia mountain mint were visited by honey bees for 45 days or less (Table 3). However, only two populations of pilose mountain mint have been evaluated, and these have not been evaluated for all three years. On the basis of these data, it would be worthwhile to test additional populations of pilose mountain mint.

Sage

Twelve populations of Pitcher's sage were evaluated in the test plot. This species was selected for its ability to flower later in the summer than the other genera. This species did not overwinter well

Table 2. Populations preferred by honey bees.

Species	*Population*	*Origin*	*BVI*
1987			
Anise hyssop	A4550	Wild: Barnes Co., ND	145.1
Anise hyssop	A4576	Cultivated: Carver Co., MN	135.6
Korean-mint	A4721	Cultivated: Idaho	133.2
Anise hyssop	A4546	Cultivated: Story Co., IA	110.1
Korean-mint	A4992	Cultivated: Polk Co., IA	108.4
Anise hyssop	A3064	Cultivated: Manitoba	98.5
Anise hyssop	A3481	Cultivated: Washtenaw Co., MI	87.4
Catnip giant hyssop	A4716	Wild: Iowa	80.7
Virginia mountain mint	A4964	Wild: Delaware Co., PA	67.5
Virginia mountain mint	A4577	Cultivated: Carver Co., MN	34.2
1988			
Korean-mint[1]	A4992	Cultivated: Polk Co., IA	287.1
Korean-mint[1]	A7722	Cultivated: Quebec	195.5
Korean-mint[1]	A4721	Cultivated: Idaho	191.2
Anise hyssop	A4550	Wild: Barnes Co., ND	156.4
Anise hyssop	A7611	Wild: Hennepin Co., MN	147.5
Anise hyssop	A7765	Wild: Manitoba	124.3
Anise hyssop	A3064	Cultivated: Manitoba	116.9
Korean-mint[1]	A5018	Cultivated: Ingham Co., MI	101.2
Anise hyssop	A4576	Cultivated: Carver Co., MN	100.2
Anise hyssop	A7569	Wild: Cass Co., MN	98.5
1989			
Korean-mint[1]	A4992	Cultivated: Polk Co., IA	1110.5
Korean-mint[1]	A4721	Cultivated: Idaho	663.2
Anise hyssop	A4550	Wild: Barnes Co., ND	241.8
Anise hyssop	A3064	Cultivated: Manitoba	241.4
Anise hyssop	A4576	Cultivated: Carver Co., MN	237.6
Pilose mountain mint	A5021	Cultivated: Ingham Co., MI	234.7
Anise hyssop	A7569	Wild: Cass Co., MN	198.1
Catnip giant hyssop	A7919	Wild: Boone Co., IA	194.3
Pilose mountain mint	A7909	Wild: Wabash Co., IL	185.5
Virginia mountain mint	A4991	Wild: Ogle Co., IL	185.0

[1] Hybrids between Korean-mint and anise hyssop replaced Korean-mint during 1988 and 1989 (see text). In such cases, the population number and origin listed refer to the seed parent of the hybrids.

in 1986-1987 (Widrlechner 1987) and seems to be susceptible to a wilt disease in wet summers.

In the test plot, consistent flowering did not occur until the end of August (Table 3). Even during peak flowering, the plants were not visited by many honey bees (Table 1). Bumble bees visited the flowers frequently, and, as with bee balm, these flowers are shaped to reward insects with tongues longer than those of honey bees.

CONCLUSION

This preliminary field evaluation of honey bee preference for native, perennial mint family plants consistently ranked populations of giant hyssop and mountain mint better than those of bee balm and Pitcher's sage. These evaluations were conducted over a three-year period, but in only one site. The most promising populations

Table 3. Season of peak honey bee visitation.

	Evaluation period					
Species evaluated	*Late June*	*Early July*	*Late July*	*Early August*	*Late August*	*Early September*
Anise Hyssop	XX[1]	XXX	XX	XX	XX	X
Korean-mint and Hybrids[2]	x	X	XXX	XXX	XXX	XXX
Catnip giant hyssop			x	XXX	XXX	X
Bee balm	x	x	x	x		
Horsemint	x	x	x	x		x
Pilose mountain mint		x	XXX	XXX	X	x
Slender-leaved mountain mint	x	XX	X	x		x
Virginia mountain mint	x	XXX	XX	x		x
Pitcher's sage					x	x

[1] Key to symbols: x = flowering with little honey bee activity, X, XX, XXX = relative intensity of honey bee visitation.

[2] Hybrids between Korean-mint and anise hyssop replaced Korean-mint during 1988 and 1989 (see text).

from these preliminary trials will be evaluated in a replicated trial under various field conditions. Populations that perform well under a wide range of conditions can be used to provide nectar for the large number of honey bees employed by the NCRPIS and may also be useful for plantings to help support commercial beekeeping.

ACKNOWLEDGMENTS

I would like to thank Drs. Dan Mayer, John Pleasants, and Randy Shoemaker for their helpful critiques of this manuscript. And I am especialy grateful to all the workers who have counted bees and have maintained the test plot.

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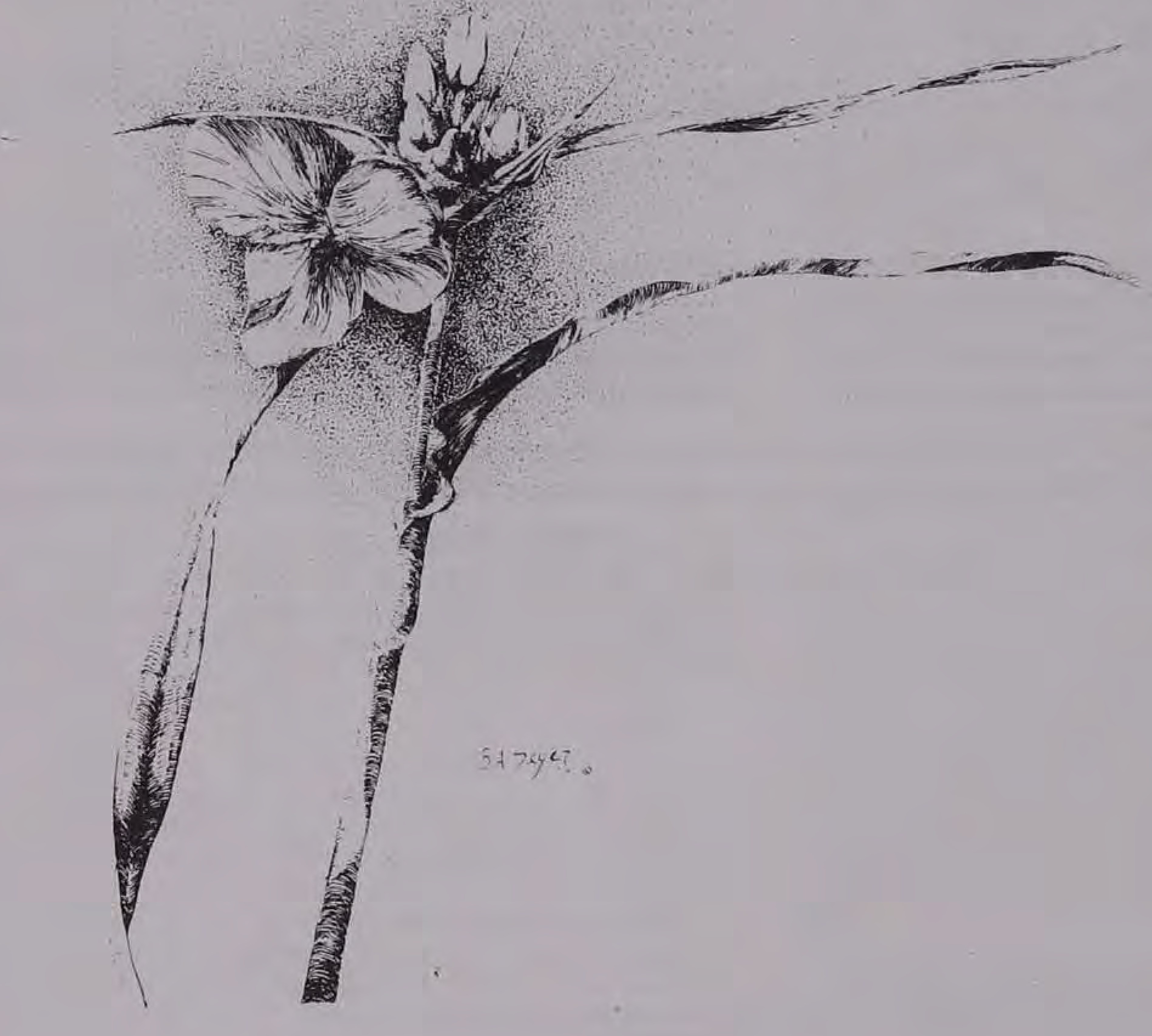

EFFECTS OF PLAINS POCKET GOPHERS ON ROOT BIOMASS AND SOIL NITROGEN

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Abstract. Total nitrogen and root biomass in 60 cm soil cores from plains pocket gopher den and food cache sites were compared to cores from control sites. Locations of den sites and food caches were determined from monitoring radio-tagged gophers. Control sites were located 5 m north of gopher sites and were assumed to have minimal gopher activity other than feeding. Gopher activities at den sites and food caches appeared to reduce total nitrogen in the top 10 cm of soil, but increased total nitrogen from 11-60 cm, especially at the level of primary tunnels (21-40 cm) and dens (51-60 cm). The decrease in total nitrogen in the top 10 cm soil zone probably resulted from gophers moving soil from lower levels to the surface when building mounds. Increases in total nitrogen in zones below 11 cm could have resulted from urine, feces, and decomposing plant parts left in food caches, tunnels, and dens.

INTRODUCTION

Plains pocket gophers, *Geomys bursarius* (Shaw), live in a three-dimensional subterranean habitat with burrows located from a few cm below the surface for feeding, to more than 50 cm deep for nest chambers (Scheffer 1940). Pocket gophers have the potential to markedly affect plant communities because digging and filling burrows changes the location of soil resources (Huntly and Inouye 1988, Reichman et al. 1982). Several studies have documented changes in surface soil characteristics as a result of mound building activity. Grant et al. (1980) found a short-term decrease in plant production proportional to the area covered by mounds. This created a mosaic of patches in various stages of secondary succession. Grant and McBrayer (1981) examined the nutrient status of soil in pocket gopher mounds and found an increase in the availability of cations from the decay of buried plant material. Tilman (1983) concluded that food preferences of gophers and the rapid growth of annual forbs on gopher mounds tended to confound the direct effects of experimental manipulation of nutrients. Addition of nutrients increased plant production, but consumption by gophers masked the increase. Inouye et al. (1987b) found that gophers reduced average soil nitrogen near the surface and increased point-to-point heterogeneity of surface soil nitrogen by moving nitrogen-poor subsurface soil to the surface when building mounds.

Our study site, Old Field 42, was located at the Cedar Creek Natural History Area, 55 km north of Minneapolis, Minnesota. The Sartell soil association, formed in fine, sand-textured glacial outwash and aeolian sediments, was light colored, undulating to hilly, and excessively drained (Grigal et al. 1974). Old Field 42 was clear-cut and farmed about 1910. The last known crop, in 1951, was clover. After 34 years of lying fallow, vegetation in Old Field 42 consisted primarily of Kentucky bluegrass (*Poa praetensis* L.), little bluestem (*Schizachyrium scoparium* (Michx.) Nash), big bluestem (*Andropogon qerardi* Vitman), and prairie forbs. We presume gopher presence in this field coincided with the advent of agriculture.

Locations of 22 den sites and 8 food caches were known from a radio-telemetry study of gopher behavior conducted from October 1983 through September 1985 (Zinnel 1992). Runways 25-35 cm deep, which connect den sites and foraging areas, remain in permanent use (Scheffer 1940). In this paper, den site refers to a discrete location at the confluence of several permanent tunnels and contains the primary nest chamber. Topology over den sites consisted of a tussock or hillock slightly raised above an otherwise uniform surface. Den sites and food caches were small distinct locations where gophers spent more than 50% of their time (referred to as gopher use areas).

We compared total nitrogen and root biomass in the top 60 cm of the soil profile at these sites with nearby control sites. Our basic premise was that available nitrogen was correlated with total nitrogen. Thus, an increase or decrease in total nitrogen should be reflected in a corresponding increase or decrease in root biomass. This relationship is based on data showing that total above-ground biomass in Cedar Creek old fields increased significantly with soil nitrogen (Inouye et al. 1987a).

METHODS

Soil cores were taken from 22 presumed den sites and 8 presumed food caches in October 1985. Soil cores taken 5 m north of each of the first sample sites were used as controls. Because of the sandy nature of the soil, compaction did not occur while taking the core. If a tunnel was encountered when taking the soil core, an alternate sample site was selected. Paired soil cores were known to be from the same gopher home range, but the 5 m separation was believed adequate to ensure that the control was not part of the den site or food cache.

Telemetry data were accurate to 1 m and allowed the den sites and food caches to be very precisely located. For example, the 4 m^2 area surrounding the den typically contained 40-50% of all locations. An area of 9 m^2 contained 66-76% of all locations. However, expanding this area to 25 m^2 added only an additional 1-4% of the locations (Zinnel 1992). Food caches were also identified as concentrations of telemetry locations. However, because the surface relief was not typical of gopher dens, these sites were inferred to be food caches.

Each sample site was further classified on the basis of telemetry data as to whether it had been used by a gopher either more or less than 50% of the time since the location was first known. Sites used more than 50% were classified as usually occupied; those used less than 50% of the time were classified as usually vacant. A further criterion for selection of sample sites was lack of disturbance caused by trapping or badger digging.

The 3.4 cm diameter soil cores were cut into six 10 cm samples, as measured from the surface. Volume of each 10 cm sample was 90.79 cm^3. Each sample was oven dried at 40C to constant mass. Root material was separated with a 1 mm mesh sieve, weighed to 0.001 g, and expressed as root biomass per 1000 cm^3 of soil. Total nitrogen, expressed as ppm/g of soil after roots were removed, was determined colorimetrically using an alkaline persulfate digestion technique (Tilman 1983) with a Technicon Auto-Analyzer. Accuracy was within 3%, as determined by analysis of 32 duplicate samples. Analysis of differences in root biomass and total nitrogen between den sites or food caches and corresponding controls was performed using the SPSS paired t-test procedure and a 2-tailed probability test (Nie et al. 1975).

RESULTS

Food Cache Sites

At food caches total nitrogen was reduced 33% in the 1-10 cm zone compared to controls ($P < .031$) (Figure 1B) . Total nitrogen was significantly higher compared to control sites at 11-20 cm ($P < .037$), 21-30 cm ($P < .001$), 31-40 cm ($P < .027$), 41-50 cm ($P < .020$), and 51-60 cm ($P < .050$) . Thus, total nitrogen was reduced at the surface but was significantly higher at every zone below 10 cm at the food cache sites. This pattern could result from release of nutrients during decomposition of uneaten food caches.

No significant differences in root biomass could be detected at any depth at food cache sites (Figure 1A). The high average root biomass in the 21-30 cm zone is the result of sampling through food caches. Some of the stored plant material became part of the root biomass sample. There is also a large standard error at this depth because half of the caches were vacant at the time of sampling. This resulted in a non-significant t-test, despite the high average root biomass for food caches as compared to control sites.

Occupied Den Sites

Total nitrogen was not significantly reduced in the 1-10 cm zone at usually occupied den sites compared to control sites (Figure 2B). Average root biomass was higher compared to control sites, although not significantly (Figure 2A). Root biomass was significantly higher in the 11-20 cm zone ($P < .005$) at usually occupied den sites compared to control sites, but no significant effect was found for total nitrogen at this depth. Conversely, we found a significant increase in total nitrogen but not in root biomass at 21-30 cm ($P < .013$), 31-40 cm ($P < .004$), and 51-60 cm ($P < .041$) at usually occupied den sites compared to control sites. As indicated above, these depths are characteristic of primary tunnels and nest chambers. The intervening layer, 41-50 cm, between tunnel and den site depths, showed no significant difference compared to control sites for either total nitrogen or root biomass.

Vacant Den Sites

In the 1-10 cm zone at usually vacant den sites, a significant decrease in total nitrogen ($P < .042$) occurred with a corresponding significant decrease in root biomass ($P < .008$) (Figure 3). No significant differences were seen for total nitrogen or root biomass from 11-20 cm, 41-50 cm, or 51-60 cm. However, both total nitrogen and root biomass showed a significant increase ($P < .028$ and $P < .001$, respectively) in the 21-30 cm zone. Total nitrogen was also significantly higher ($P < .0001$) at 31-40 cm near usually vacant den sites. Root biomass was not different from paired controls at this depth.

DISCUSSION

Because the study site was in glacial outwash sand plain of uniform deposition, initial conditions for the paired soil cores were assumed to be equal. Therefore, measured differences in total nitrogen and root biomass were assumed to reflect modification by gophers.

Reichman and Smith (1985) found 33% lower plant biomass over active gopher burrows compared to control sites. However, they concluded it might take decades for this effect to create significant differences in vegetation between areas with gophers compared to areas without gophers. They found the greatest above-ground plant biomass adjacent to active burrow systems and concluded that gophers chose to burrow in the most productive areas.

Figure 3A shows a significant decrease in root biomass in the 1-10 cm zone near usually vacant den sites compared to control sites. This decrease may be due to over-grazing by gophers, leading to temporary abandonment of the den sites. Comparing average root biomass from the 1-10 cm zone at usually occupied den sites (Figure 2A) to biomass from usually vacant den sites (Figure 3A) also suggests that gophers occupied the most productive areas. Average root biomass values for usually occupied den sites were higher than those of usually vacant den sites.

Owens and Wiegert (1976) proposed that consumers, like pollinators, have a mutualistic relationship with plants. Increased root biomass around den sites would support this hypothesis. Significant increases in root biomass and total nitrogen at den sites, as compared to less frequently used areas, occurred at 25-35 cm, the depth of main tunnels connecting other parts of the gopher home range with the actual nesting chamber (Scheffer 1940).

Soil movement by gophers may change soil compaction, thus allowing roots to penetrate deeper. Evidence supporting this was the significant increase in root biomass at 11-20 cm and 21-30 cm at den sites compared to controls.

We suspect that gophers harvest roots in the vicinity of den sites. This may explain why the significant increases in total nitrogen did not always have corresponding increases in root biomass. Because gophers spend more than 50% of their time in the den site area, and den sites are used repeatedly by a succession of gophers, this effect could be considerable.

Grant and McBrayer (1981) reported that freshly buried plant parts in gopher mounds increased the availability of cations and appeared to have a green-manure effect. Nitrogen concentration in new mounds averaged 650 ppm, with a range of 500 to 980 ppm. These values are comparable to our data. Their October sampling recorded new mounds as having more, freshly buried plant parts than old mounds and control sites combined. All of our food cache samples were also taken in October. Thus, nutrient influx phenomena should be comparable. Significantly higher total nitrogen at all depths below 11 cm in the vicinity of food caches (Figure IB) may result from decay of plants stored by gophers.

If increases in total nitrogen at den sites were due solely to gophers redistributing the high-nitrogen surface soil to lower depths when filling abandoned burrows and to gophers moving low-nitrogen soil to the surface when building mounds, the sum of all the nitrogen samples for all depths should be similar for den versus control sites. This is not the case. The sum of nitrogen measurements at all zones for den sites is 11% higher than for control sites situated 5 m away. We propose that gopher urine, feces, and decomposing uneaten food could account for the increase in total nitrogen in the 21-30 cm, 31-40 cm, and 51-60 cm zones at den sites.

Increased total nitrogen at nest chamber depth (51-60 cm) was associated with usually occupied den sites, but not with usually vacant den sites. Concentrations of feces, urine, and plant parts near the den may have been the source of this nitrogen. Telemetry data indicated that non-resident gophers investigated unoccupied den sites. These transient gophers may have deposited feces and urine near the den, perhaps as scent marks. Because of historical use by generations of gophers, den sites appear to be a valuable resource.

Gopher activities in the 1-10 cm zone at or near den sites and food caches appeared to reduce total nitrogen when compared to control sites, which were used less frequently. We concluded that this was caused by gophers moving soil with low nitrogen content from deeper levels to the surface when building mounds and by gophers removing surface vegetation while foraging.

Gophers may benefit by maintaining conditions favorable for early successional species. Tilman (1983) found significant positive correlation between above-ground plant biomass and gopher activity. This supports the mutualism hypothesis of Owens and Wiegert (1976) in that mounds characterized by low nitrogen and high light would be dominated by early successional species. Some of these species, such as annual forbs, are favored by gophers as food items (Behrend and Tester 1988).

It is apparent that pocket gophers may have a large impact on soil fertility and, consequently, on the plant community. Impacts of mounds and castings have been well documented. Data presented here provide new information on the impact of den sites and food caches on soil fertility and root biomass.

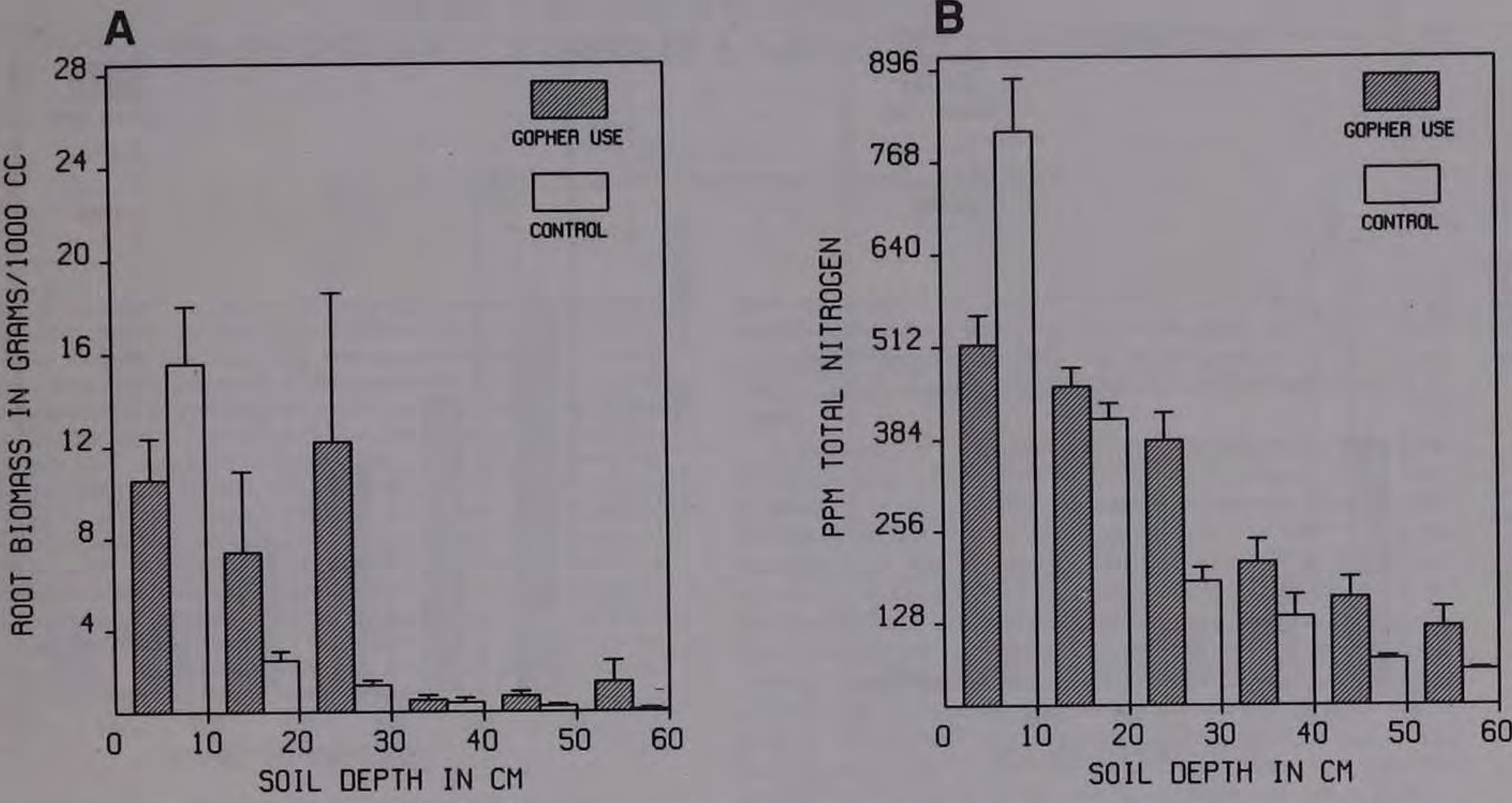

Figure 1. Root biomass (A) and total nitrogen (B) at various soil depths at eight pocket gopher food caches and paired control sites.

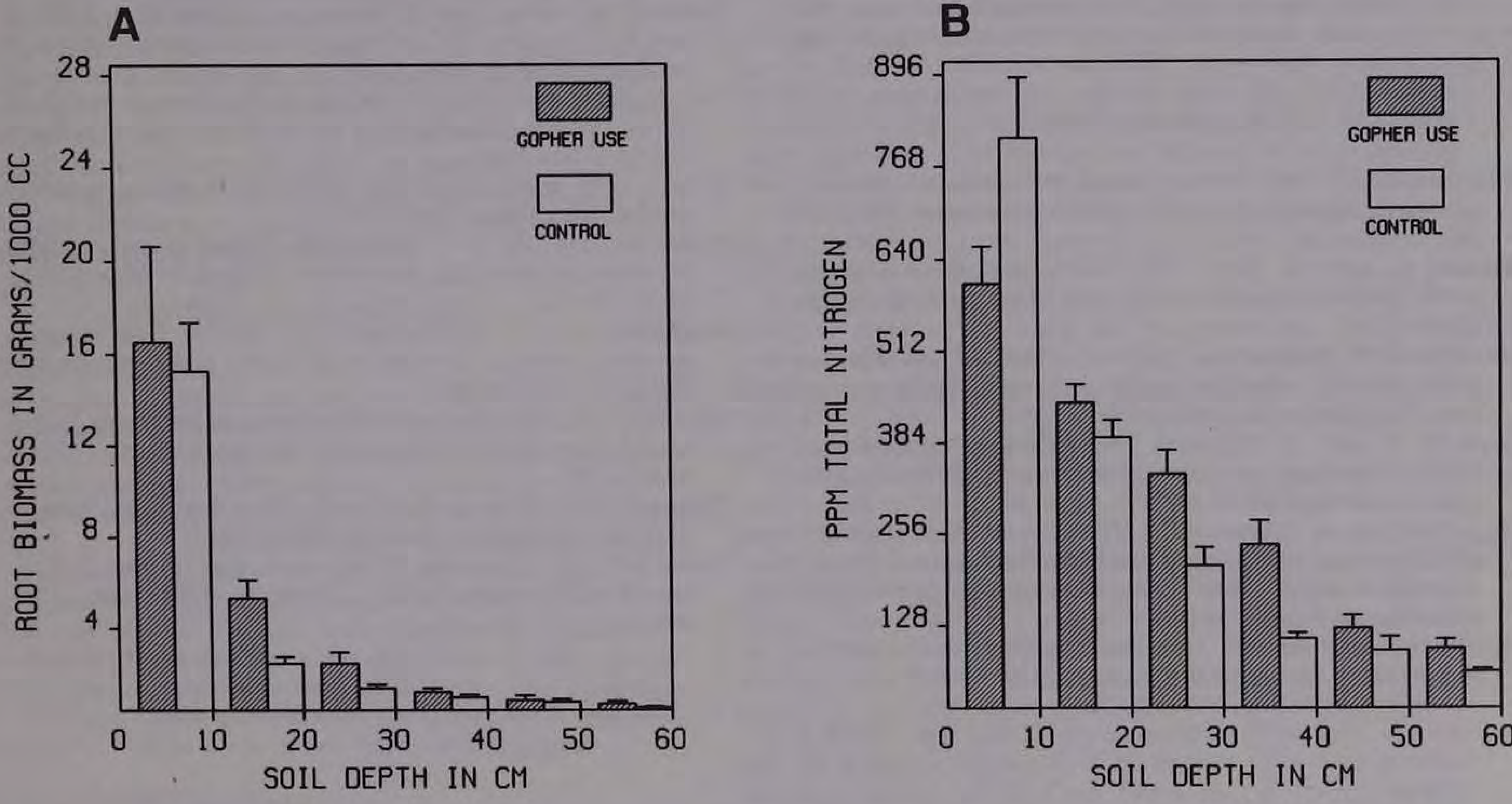

Figure 2. Root biomass (A) and total nitrogen (B) at various soil depths at 11 usually occupied pocket gopher den sites and paired control sites.

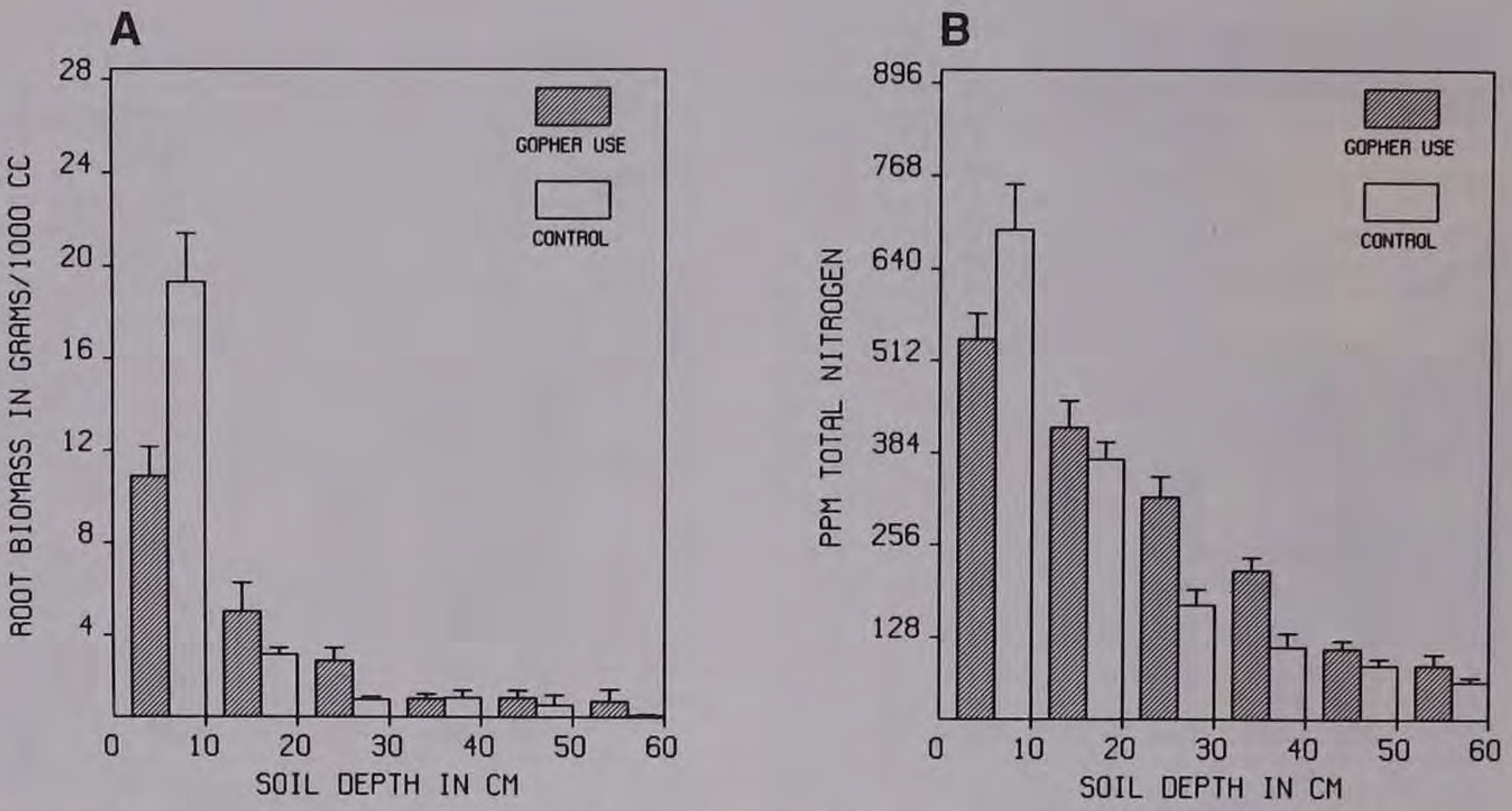

Figure 3. Root biomass (A) and total nitrogen (B) at various soil depths at 11 usually vacant pocket gopher den sites and paired control sites.

ACKNOWLEDGEMENTS

Funds for this project were provided by NSF grant DEB 8114302 (LTER) awarded to G. D. Tilman and J. R. Tester. We thank Cedar Creek Natural History Area for logistic support and facilities.

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THE EFFECTS OF POCKET GOPHERS ON SURVIVORSHIP, GROWTH, AND REPRODUCTION OF LARGE BEARDTONGUE

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Abstract. A three-year study examined how pocket gophers affect patterns of survivorship, growth, and reproduction of large beardtongue (*Penstemon grandiflorus*, Scrophulariaceae). With their mound-building and tunneling behavior, pocket gophers create areas with sparse vegetation. Plants growing naturally in areas with pocket gopher disturbances exhibited higher rates of mortality, but surviving plants grew faster and reproduced sooner than other plants. In an experiment in which beardtongue was transplanted into two gopher-proof pens, one with and one without other vegetation, plants growing in the pen with bare soil exhibited higher rates of survivorship, growth, and reproduction, compared to the plants in the naturally vegetated pen. A root-removal experiment designed to simulate gopher herbivory showed that root loss of a kind normally experienced by beardtongue resulted in higher rates of mortality. However, reproduction in surviving plants was not affected by root removal. The data show that although pocket gophers reduce the survivorship of individual plants, their presence actually helps perpetuate large beardtongue in the landscape.

INTRODUCTION

In the North American prairie and adjacent oak savanna habitats, pocket gophers were important agents of disturbance prior to European settlement (Mielke 1977). Through their earth moving activities, pocket gophers and other fossorial animals modify the prairie and savanna landscape in several ways, including the creation of soil mounds, feeding tunnels, and underground food caches. These features have been found to influence the survivorship, recruitment, growth, reproduction, and biomass of the surrounding vegetation (Platt 1975, Tilman 1983, Hobbs and Mooney 1985, Reichman and Smith 1985, Reichman 1988). Feeding principally on herbaceous plants (Behrend and Tester 1988), pocket gophers can also affect the vegetation through their herbivory. The purpose of this study was to determine the extent to which pocket gophers affect survivorship, growth, and reproduction of large beardtongue (*Penstemon grandiflorus* Nutt., Scrophulariaceae) through their herbivory and mound building.

MATERIALS AND METHODS

The Study Area and Plant

The study area comprises approximately 25 ha of oak woodland and savanna located at Cedar Creek Natural History Area, East Bethel, Minnesota. Cedar Creek is situated on a 2,200 sq km sand plain formed 12,000 to 13,000 years ago by glacial outwash at the end of the Wisconsin glaciation. Large beardtongue is a perennial forb which grows in well-drained, usually sandy, habitats, principally in the eastern portion of the Great Plains (Great Plains Flora Association 1986). First-year beardtongue plants usually consist of a single leafy rosette. The size, and sometimes the number, of rosettes increases with age, and a flowering stem, or stems, can be produced during the second or subsequent years. After flowering once, plants may flower again the next year or may revert back to a rosette growth form for a year or two before flowering again.

Tagging and Monitoring of Plants

In 1986, 28 flowering stems located in openings in the woodland were randomly selected, and each was used as the center of a circular plot (4 m diam). These 28 stems and all beardtongue in the plots were tagged, for a total of 941 plants. In order to increase the number of flowering plants included in the study, additional flowering plants throughout the study area were tagged in 1986 (107) and 1987 (1,098) and marked with stakes to facilitate subsequent relocation.

In summer 1987 and 1988, previously tagged plants were located. If the plant was present, its growth form (stem or rosette) was recorded. For rosette plants, the number of rosettes for each plant was also recorded, and the maximum diameter of each rosette was measured. For stem plants, the number of stems for each plant was recorded, and the height of each stem was measured. For some of the comparisons, rosette plants were grouped into one of four size classes based on the measurment of the total rosette diameter (*small rosettes*: less than 9.0 cm; *medium rosettes*: 9.0-13.9 cm; *large rosettes*: 14.0-20.9 cm; and *extra-large rosettes*: 21.0 cm or greater). Stem plants were similarly divided into three size classes based on total stem height of all stems (Small Stems: less than 48.0 cm; Medium Stems: 48.0-59.9 cm; Large Stems: 60 cm or greater). The size intervals used for both rosette and stem plants were selected to produce size categories with approximately equal numbers of plants in 1986.

Measuring Effects of Surrounding Vegetation on Survivorship, Growth, and Reproduction

In environments inhabited by pocket gophers, the presence of bare soil in an area is a good indication of current or recent gopher activity (Foster and Stubbendieck 1980). In my study, gophers are the primary cause of bare soil, although thatch ants, which produce soil rings around their mounds, are minor contributors. In order to determine if rates of beardtongue are different for plants growing where gophers are active, the percent cover of bare soil within 20 cm of each plant was measured by using a point frame method (Bonham 1989). The total number of pins (0-20) touching bare soil was recorded for each plant.

Based on these measurements, plants were divided into two groups of approximately equal size for comparison. Plants with bare-ground cover estimates equaling or exceeding 20% were defined to be growing in sparsely vegetated areas. Plants with bare-ground cover estimates less than 20% were defined to be growing in densely vegetated areas.

To test the effect of surrounding vegetation on survivorship, growth, and reproduction in the absence of gophers, a separate experiment was begun in July 1989. One hundred twenty beardtongue were transplanted into two previously existing gopher-proof pens (10 m diam) located in an old field at Cedar Creek (Lampe 1976). These pens were 2 m apart, and both were overgrown with old field vegetation. Analysis of soil cores from each pen showed that the soil in the two pens did not differ in percent total nitrogen or carbon. Two weeks prior to the experiment, all the vegetation in one of the pens was killed using an herbicide (*Roundup*). In each pen, the transplants consisted of 60 large or extra-large rosettes excavated from a field at Cedar Creek and 60 smaller rosettes which had been germinated from seed in spring 1989. In both pens, the two size classes were planted alternately in a grid pattern. All plants were tagged and measured following transplanting in July

1989. In June 1990, the plants were remeasured, and the reproductive status of all surviving plants was recorded.

Measuring Effects of Root Loss on Survivorship, Growth, and Reproduction

Previous laboratory observations of captive gophers showed that although pocket gophers readily eat the fleshy beardtongue roots, they generally avoid the woody caudex, stem, and leaves (unpublished data). To simulate root herbivory in the field and to measure the effect of root loss on plant survivorship, growth, and reproduction, a root-pruning experiment was conducted in August 1988. In this experiment, 45 plants were carefully excavated and assigned to one of three treatments: no root removal, 25% root removal, and 75% root removal. The roots of plants assigned to one of the two root removal classes were pinched off at the caudex until an estimated 25%, or 75% of the root mass had been removed. All plants were transplanted immediately following root removal. An identical experiment was conducted in June 1989.

In summer 1989 (June for the first experiment, July for the second), the number of surviving plants in each treatment was recorded for both experiments. The proportion of surviving transplants which had flowered was also recorded for each of the three treatments. In addition, the fruiting stems were collected for later analysis of reproductive output. The total volume of the pods produced by a plant was used as a measure of pod volume. Pod volume was estimated by first measuring the area of a pod and then using the formula of a cone to convert the area into a volume estimate. Area was measured from overhead with the pod lying on its side and using image analysis software (Olympus Corporation) and a Zeos 286 computer with a video camera attachment. Pod volume was highly correlated with seed production, (r=.88, p<.001, n=11).

RESULTS

Survivorship

Effects of plant size.

Mortality rates in rosette plants, non-reproductive individuals,decreased with increasing size of the rosette (small rosette: 36.2%, n= 229; medium rosette: 24.8%, n=266; large rosette: 14.2%, n=295; extra large rosette: 7.6%, n=237; G=128.5, p<.001), using Log-Likelihood Ratio Test for Contingency Tables, (Zar 1974).

Effects of vegetation cover.

Overall, plants growing in sparse vegetation, as determined by the point frame method, sustained significantly higher rates of mortality (25.3%, n=648) than did plants growing in densely vegetated areas (12.5%, n=945; G=41.78, p<.0001). There was a significant positive correlation between the percent coverage of bare ground in the 28 plots established in 1986 and the mortality rate of the plants in those plots during the subsequent year, r=.50 (Spearman), p<.02. There was also a significant positive correlation between bare ground coverage and density of beardtongue in the 28 plots, r=.42, p<.05.

In the experimentally devegetated, gopher-proof pen, survivorship of transplanted beardtongue (91.8%) was significantly greater than in the naturally vegetated control gopher-proof pen (68.8%), G=18.08, p<.001.

Effects of mound building by gophers.

During this study, 66 plants were determined to have been killed by being buried under the mounds made by pocket gophers, for an annual burying rate of 2.2%, n=3020. Rosette plants represented all but three of the buried and killed plants and were significantly more likely to be killed by burying than were stem plants (3.8%, n=1,662 for rosette plants versus 0.2%, n=1,358 for stem plants, G=53.816, p<.001). Overall, buried and killed rosettes were smaller in diameter than other rosettes (13.68 ± 1.40 cm, n=63 for buried versus 19.59 ± .36 n=1,599 for nonburied, t=3.27, p<.002; SE provided, data log transformed before analysis). The annual probability of being buried and killed for small and medium rosettes was 7.6%.

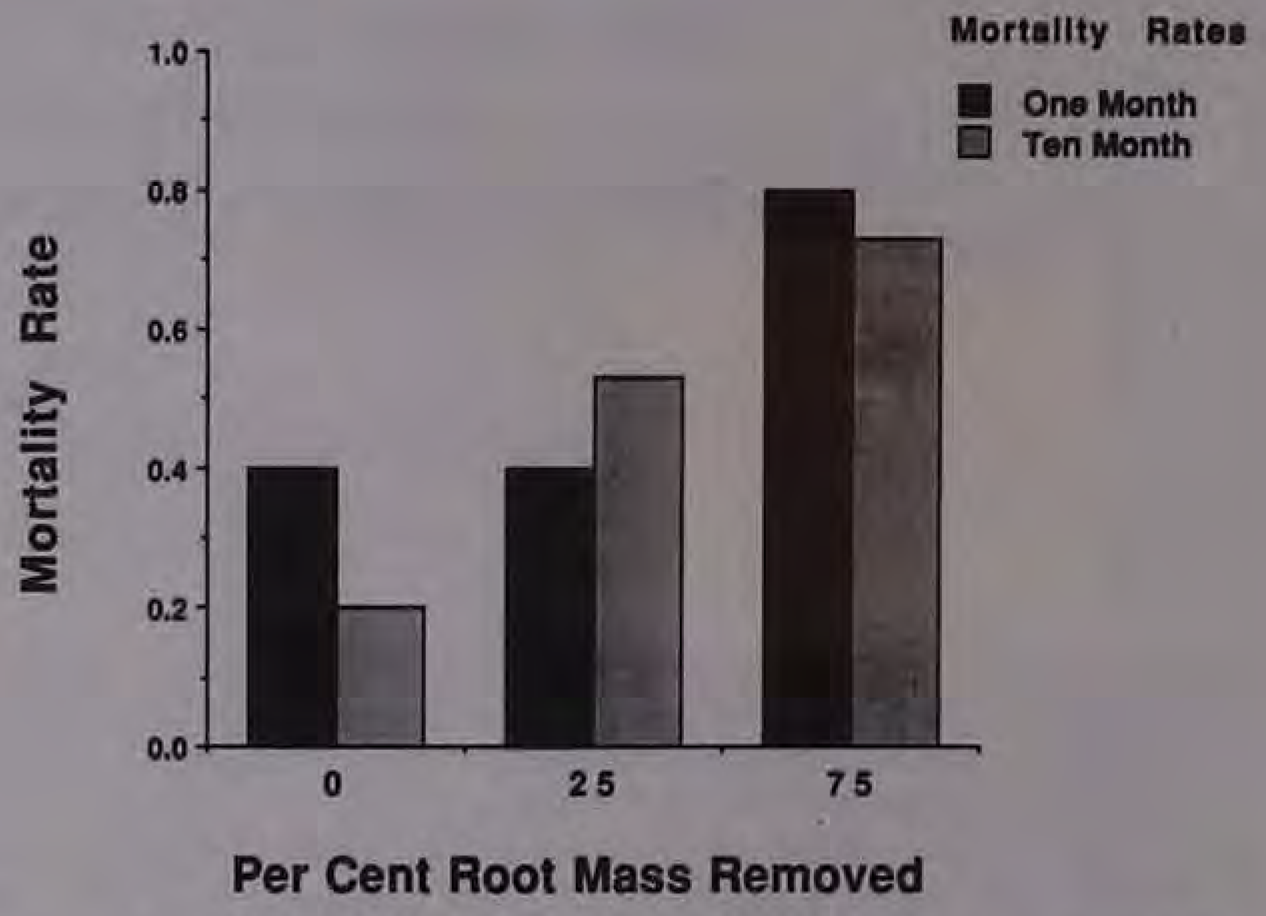

Figure 1. Mortality rates for beardtongue plants in which 0%, 25%, or 75% of the root mass had been experimentally removed. Shown are the results for two separate experiments, one in which survivorship was recorded 10 months following root removal, and one in which it was recorded 1 month following root removal. Sample size in both experiments was 45 (15 in each treatment).

Effects of root removal.

Removal of root tissue significantly reduced survivorship of beardtongue (Figure 1). This was true both ten months following root removal (G=9.26, p<.01; first experiment) and one month following root removal (G=6.79, p<.05; second experiment). There was no transplant effect with respect to survivorship (mortality rate of transplanted controls: 30%, n=30; mortality rate of comparably sized nontransplanted plants: 17.3%, n=243, G=1.88, p>.10).

Reproduction

Effects of plant size.

The probability of flowering increased with plant size (small rosette: 1.3%, n=151; medium rosette: 5.6%, n=198; large rosette: 30.4%, n=250; extra-large rosette: 79.3%, n=222; stem plants: 62.9%, n=491). Similarly, the total height of flowering stem(s) produced by a rosette plant increased with rosette size (r=.287, p<.001, n= 551). The number of flowering nodes on a stem was significantly correlated with the height of the stem (r=.803, p<.001, n=1,020). Thus, large plants were more likely to flower and to produce larger inflorescences than were small plants.

Effects of vegetation cover.

The rate of reproduction in plants growing naturally in sparsely vegetated areas (39.6%, n=492) did not differ significantly from that of plants growing in densely vegetated areas (42.8%, n=817; G=1.17, p>.25). The relative proportions of large, medium, and small flowering stems in densely vegetated areas (n=350) also did not differ from those in sparsely vegetated areas (n=139; G=1.66, p>.10).

Plants transplanted into the experimentally devegetated, gopher-proof pen reproduced at a significantly higher rate than did plants in the vegetated control pen (devegetated pen: 69.7%, n=109; control pen: 31.7%, n=82; G=26.2, p<.001; percentages based on surviving plants).

Effects of root removal.

The transplanting procedure did not affect the probability of reproducing in beardtongue (control transplants: 58.3%, $n=12$; comparably sized nontransplanted plants: 47.2%, $n=197$; $G=0.204$, $p>.50$). Because of the low rate of survivorship in root-pruned plants, the two pruning treatments were grouped for the analyses of reproduction. Root pruning did not affect the rate of flowering in the surviving transplants (root-pruned plants: 81.8%, $n=11$; control plants: 58.3%, $n=12$; $G=0.599$, $p>.25$). Root pruning also did not affect the plant reproductive output as measured by total volume of pods produced (root-pruned plants: 1,305.7 + 272.2 mm^3, SE, $n=9$; control plants: 1,297.1 ± 350.9 mm^3, $n = 7$; $t=.015$, $p>.50$).

Growth

Effects of vegetation cover.

The likelihood that a plant would increase in size class was significantly greater among plants growing in sparsely vegetated areas than among those growing in densely vegetated areas (X2 = 7.77, $p<.005$). Plants transplanted into the experimentally devegetated, gopher-proof pen were significantly more likely to increase in size class than plants in the vegetated control pen (devegetated pen: 94.5%, $n=109$; control pen: 64.6%, $n=82$; $G=26.7$, $p<.001$, percentages based on surviving plants).

Effects of root removal.

Because most of the plants which survived the root removal treatment flowered the following year, and because the production of a stem is considered an increase in size class, the conclusion regarding the effect of root removal on growth is identical to that for reproduction: no effect. Too few surviving plants remained rosettes to permit a separate analysis of the effect of root removal on growth of plants which did not reproduce.

DISCUSSION

Herbaceous plants of grasslands and savannas regularly experience a variety of disturbances, including soil excavation by fossorial animals and herbivory both above and below ground (Mielke 1977, Behrend and Tester 1988, Gibson 1989, Contreras and Gutierrez 1991). Through their differential effects on survivorship, growth, and reproduction of individual plants of different species, these disturbances can influence the community composition of the vegetation (Platt 1975). The results reported in this paper show that pocket gophers can significantly increase mortality in one forb species, large beardtongue, through their mound-building activities and possibly through their underground herbivory. At the same time, however, plants which are growing where gophers are active grow faster and reproduce sooner. In addition, the density data presented, along with other preliminary data on recruitment (unpublished), indicate that recruitment is higher in gopher areas than in areas where gophers are not active and where there is little bare soil.

Thus, although pocket gophers reduce survivorship of beardtongue plants in affected areas, they appear to help perpetuate large beardtongue in the larger landscape. In addition, the gophers can be viewed as altering their environment in a way which enhances the growth, reproduction, and recruitment of a food plant.

ACKNOWLEDGEMENTS

This study was supported by NSF Grant BSR-8717847; by a grant from the Minnesota Private College Research Foundation with funds provided by the Blandin Foundation of Grand Rapids, Minnesota; by grants from Cedar Creek Natural History Area, which is managed by the University of Minnesota in cooperation with the Minnesota Academy of Science; and by grants from Macalester College with funds provided by the Bush Foundation and the Wallace Foundation. Kirsten Banks, Jodi Buckman-Fifield, Jon Dicus, Susan Hofmann, Sarah McAndrew, Heidi Scholtz, Jeff Villinski, and Elisabeth Young helped collect much of the data.

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POPULATION ECOLOGY OF THIRTEEN-LINED GROUND SQUIRRELS IN UNGRAZED TALLGRASS PRAIRIE MANIPULATED BY FIRE

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Abstract. From March 1983 to October 1987, thirteen-lined ground squirrels (*Spermophilus tridecemlineatus* Mitchill) were studied in ungrazed tallgrass prairie manipulated by fire on the Konza Prairie Research Natural Area, Kansas. Overall abundance varied among years (2.6 animals/ha in 1985; 5.6 animals/ha in 1986); however, no significant variation in sex ratio was observed (overall average = 52% males for adults, 48% males for juveniles). Fire had a positive effect on ground squirrels; abundance was significantly higher in burned than unburned prairie during the year of a fire and in more recently than less recently burned prairie during years following a fire. Ground squirrels also selected hillsides with exposed rocks (breaks) over upland and lowland prairie sites. Although females and males selected similar habitats, home ranges were significantly larger for adult males (average = 0.56 ha) than for adult females (0.36 ha). Both adult females and males caught on the study area typically were residents rather than transients. Further, overwinter survival did not differ between adult females and males. Overwinter survival of juvenile females was similar to adults; however, no juvenile males overwintered on the study area.

INTRODUCTION

Thirteen-lined ground squirrels (*Spermophilus tridecemlineatus* Mitchill) are common in grassland habitats throughout the Great Plains of the central United States (Jones et al. 1985, Streubel and Fitzgerald 1978). Although present in many grassland habitats, these ground squirrels are most abundant in native shortgrass or moderately grazed to overgrazed midgrass prairies and anthropogenic habitats, including cemeteries, mowed roadside ditches, golf courses, parks, and lawns (Abramsky et al. 1979, Andersen and Fleharty 1967, Bee et al. 1981, Choate and Fleharty 1975, Kaufman et al. 1990a, Kaufman and Kaufman 1989, Phillips 1936). Other grasslands, such as native tallgrass prairie, are used by ground squirrels, but relative densities appear to be somewhat lower than those found in habitats with short grass and limited vertical structure (Finck et al. 1986).

Tallgrass prairie once occupied about 3% of North America (Küchler 1964), but with the arrival of European settlers, much of this habitat was converted to cropland. Throughout much of the former range of tallgrass prairie, only small, disjunct patches of native prairie are found; however, the Flint Hills of southeastern Nebraska, eastern Kansas, and north-central Oklahoma are still dominated by native prairie. Presently, efforts are being made to restore tallgrass prairie in regions where nearly all native prairie was destroyed and to preserve remnant native prairies in regions such as the Flint Hills. Restoration and maintenance of prairie ecosystems require an understanding of the interrelationships of the flora, fauna, and physical environment.

The impact of management practices, such as fire, on prairie ecosystems must be better understood to help conserve the native flora and fauna. Thus, we initiated this study to examine the influence of prescribed burning and topography on the population ecology of thirteen-lined ground squirrels in ungrazed tallgrass prairie. We report on year-to-year variation in abundance, sex ratio, ratio of residents to transients, home range size, overwinter persistence, and longevity of thirteen-lined ground squirrels in tallgrass prairie of the Flint Hills of northeastern Kansas.

METHODS

Study Site

Ground squirrels were studied on the Konza Prairie Research Natural Area, a native tallgrass prairie preserve located 10 km south of Manhattan, Kansas. Konza Prairie (a 3,487-ha site) is subdivided into watersheds that are subjected to an array of prescribed burning treatments (Hulbert 1985). Dominant vegetation is characteristic of the Flint Hills region and includes big bluestem (*Andropogon gerardii* Vitman), little bluestem (*A. scoparius* Michx.) Indian grass (*Sorghastrum nutans* (L.) Nash), and switchgrass (*Panicum virgatum* L.). Rough-leaved dogwood (*Cornus drummondii* Mey.), buckbrush (*Symphoricarpos orbiculatus* Moench.), smooth sumac (*Rhus glabra* L.), New Jersey tea (*Ceanothus herbaceous* Raf. var. *pubescens* (T. & G.) Shinners), and honeylocust (*Gleditsia triacanthos* L.) are the most prevalent shrubs.

The rolling topography of the Flint Hills region is characterized by broad upland plateaus, steep hillsides, and wide lowland valleys (Jantz et al. 1975). Shallow, well-drained soils, mixed with chert and limestone fragments, are found in upland areas; whereas, lowland soils are relatively deep and mesic with few rocks. Hillsides are often terraced with limestone outcrops created by the differential erosion of alternating layers of limestone and shale. Because of this variation, each trap station on our study areas was assigned to one of three topographic positions—uplands, breaks (hillsides), or lowlands—based on slope, soil type, and presence of rock fragments.

In 1983, our study was conducted on a 5.4-ha area situated across two contiguous watersheds (4A, 2.84 ha; 4B, 2.56 ha). For 1984-1987, the study area was expanded to 13 ha situated across four contiguous watersheds (4A, 6.91 ha; 4B, 4.58 ha; 2A, 1.17 ha; WA, 0.34 ha). All of this area had been ungrazed for five years. Watersheds 4A (total area = 17.7 ha) and 4B (55.1 ha) were burned at four-year intervals (4A burned in 1980 and 1984; 4B burned in 1979, 1983, and 1987), and watershed 2A (29.6 ha) was burned at two-year intervals from 1973 to 1987. Watershed WA (26.6 ha) was burned each spring that followed a wet year—those with more than 1.2 times the expected median precipitation between 1 October and 30 September (WA burned in 1983, 1985, 1986, and 1987). All prescribed fires occurred in either April or early May of each year.

Small Mammals

During 13 March to 23 November 1983 and 4 February to 28 March 1984, small mammals were trapped on a 10 by 24 station trapping grid (15-m interstation interval; 5.4-ha study site). During 7 to 10 April 1984, an adjacent 14 by 24 station grid was trapped. The entire enlarged 24 by 24 station grid (13.0 ha) was trapped during 11 April to 2 December 1984, 9 March to 27 October 1985, 15 March to 7 November 1986, and 21 March to 28 October 1987. All traps used were large Sherman livetraps (7.6 by 8.9 by 22.9 cm); however, traps per station and frequency of trapping varied among years.

On the small grid, two livetraps were set per station on alternate rows of the grid for two days and then moved to the other set of rows

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for an additional two days of trapping. This procedure was repeated weekly during 1983, except that the trapping effort was more frequent immediately before and after the prescribed fire in spring 1983. Similarly, two traps per station for two days on alternate lines were used for 11 nights of trapping during 4 February-28 March 1984. To mark animals on the added portion of the grid in spring 1984, one trap was set per station on the 14 by 24 station area for all nights during 11-18 April, followed by one trap set per station on the entire 24 by 24 grid for eight nights during 19-29 April.

Beginning in May 1984 and continuing through 1987, one trap per station was used on alternate rows of the grid, followed by a switch to traps on the other set of rows for the next trap period. During May-December 1984, traps were set for two days, and then immediately switched for two days, with rows used first in one trap period used last in the next. Generally, these four-day periods occurred at about two-week intervals, except for more frequent trapping in May. During 1985-1987, traps were set on alternate rows for two to four nights (1985) and two nights (1986 and 1987) at about two-week intervals, except for more frequent trapping in early March 1985.

Traps were baited with peanut butter during summer and with a mixture of peanut butter and rolled oats wrapped in weighing paper during spring and autumn. Polyester fiberfill was placed in traps for nesting material during spring and autumn. Traps were closed in morning and reopened in afternoon when temperatures exceeded 29 C. In 1986 and 1987, traps being set each census period were prebaited with peanut butter (placed on the open backdoor) two days before the start of each period. Traps with back doors open were left on the grid between trapping periods.

Standard capture-mark-recapture techniques were used, with all ground squirrels uniquely toe-clipped and ear-tagged. Animals were released at their capture location after data were recorded.

Analysis

Density (individuals/ha) of ground squirrels was estimated by dividing the number of individuals by the area of the trapping grid (1983: 5.40 ha; 1984-1987: 12.96 ha). Sign tests corrected for ties (normal approximation: Z_c) were used to test for differences in density between burned and unburned prairie. The log-likelihood ratio test (*G*-test) was used to test for heterogeneity in sex ratio, proportion of residents and transients (resident = captured during more than one trap period; transient = captured during a single trap period), topographic distribution, and overwinter persistence. Yates correction for continuity was applied to 2-by-2 contingency tables, and Fisher's exact test was used when sample sizes were small. Home range size was estimated with the minimum convex polygon method (Mohr 1947). Analysis of variance (ANOVA; SAS Institute 1985) was used to test for differences in home range size between males and females. Only animals that resided on the grid area ≥ 30 days and were captured ≥ 5 times were used in this analysis. The Mann-Whitney *U*-test (chi-square approximation) was used to test for differences between males and females in time spent on the study area.

RESULTS

Between March 1983 and October 1987, 192 ground squirrels were captured. Abundance varied more than two-fold during the five years (individuals/ha = 4.82, 2.86, 2.62, 5.63, and 5.32 for each year from 1983 to 1987, respectively). Sex ratios for adults and juveniles did not differ significantly from 50% males (adults: n = 144, males = 52.1%, $G = 0.2$, $d.f. = 1$, $P > .10$; juveniles: n = 48, males = 47.9%, $G = 0.1$, $d.f. = 1$, $P > .10$). Additionally, season of the year did not affect sex ratios of adults during any of the five years ($P > .05$), nor did year of study affect sex ratios of adults or juveniles.

Ground squirrels inhabited breaks in preference to upland and lowland prairie sites (Table 1) with no differences among years ($G = 11.0$, $d.f. = 8$, $P > .10$), or between females and males ($P > .05$). However, home range size for all years combined was over 50% larger for adult males (0.56 ha) than for adult females (0.36 ha; Table 2). No difference in home range size occurred among years for either males or females ($P > .10$). Home range size was significantly greater for males (0.77 ha) than females (0.35 ha) in 1986, but no other intrayear difference was noted between the sexes.

Table 1. Numbers of thirteen-lined ground squirrels in three topographic sites on Konza Prairie.

		Topographic Site[a,b]				
Year		*Uplands*	*Breaks*	*Lowlands*	*G*	*P*
1983	Observed	7	13	16	0.9	> .10
	Expected	9.2	11.1	15.6		
1984	Observed	19	31	13	6.2	< .05
	Expected	20.6	22.2	20.2		
1985	Observed	8	27	19	9.7	< .01
	Expected	17.6	19.0	17.3		
1986	Observed	31	56	30	7.8	< .05
	Expected	38.2	41.2	37.6		
1987	Observed	29	45	30	2.9	> .10
	Expected	33.9	36.6	33.4		
Total	Observed	83	135	92	9.7	< .01
	Expected	101.2	109.2	99.6		

[a] Individual may be counted more than once if captured in more than one topographic site.

[b] Expected number of individuals based on number of trap stations within each topographic position.

Numbers of individuals per hectare were greater in burned than unburned prairie during 26 of 37 census periods in which ground squirrels were caught ($Z_C = 2.3$, $P < .05$). Similarly, this positive response to fire was evident for several years after a fire. The density of ground squirrels was greater for the most recently burned portion of the grid when compared to the area that was left unburned for the longest period during 46 of 70 census periods ($Z_C = 2.5$, $P < .05$).

Fifty-four of 69 adult females and 50 of 75 adult males were residents (Table 3). No differences in proportion of residents occurred among years for adult females ($G = 1.0$, $d.f. = 4$, $P > .10$; Table 3). However, the proportion of resident adult males did vary among years ($G = 10.0$, $d.f. = 4$, $P < .05$). This difference was due to only 25% of adult males being residents in 1983 as compared to 69% in other years. Overall, the proportion of residents was similar for adult females and males, although a difference was evident in 1983 ($P < .05$). For juveniles over all years, the proportion of residents was greater for females (48%) than males (4%; $P < .001$). Juvenile females were more likely to become residents in 1986 (77%) than 1987 (31%; $P < .05$), but no yearly differences were noted for juvenile males.

Residency time was similar for adult males and females (Table 4; all individuals: chi-square approximation = 1.4, $d.f. = 1$, $P > .10$; residents: chi-square approximation = 0.02, $d.f. = 1$, $P > .10$). For all

Table 2. Mean home range size (ha) of adult thirteen-lined ground squirrels on Konza Prairie.

	Females			*Males*		
Year	*n*	*X (ha)*	*SE (ha)*	*n*	*X (ha)*	*SE (ha)*
1983	1	0.52	-	-	-	-
1984	4	0.52	0.12	5	0.69	0.19
1985	2	0.20	0.03	4	0.50	0.13
1986	12	0.35	0.07	4	0.77	0.28
1987	9	0.31	0.08	6	0.36	0.15
Total	28	0.36	0.04	19	0.56	0.09

Table 3. Numbers of thirteen-lined ground squirrels captured on Konza Prairie between 1983 and 1987.

		Adult		*Juvenile*		
Year	*Residency*	*Females*	*Males*	*Females*	*Males*	*Total*
1983	Resident	8	3	0	0	11
	Transient	4	9	0	2	15
	Total	12	12	0	2	26
1984	Resident	12	13	1	0	26
	Transient	4	6	1	0	11
	Total	16	19	2	0	37
1985	Resident	12	13	0	0	25
	Transient	5	3	1	0	9
	Total	17	16	1	0	34
1986	Resident	20	17	7	0	44
	Transient	5	9	2	13	29
	Total	25	26	9	13	73
1987	Resident	20	14	4	1	39
	Transient	6	8	9	7	30
	Total	26	22	13	8	69
Total	Resident	54	50	12	1	117
	Transient	15	25	13	22	65
	Total	69	75	25	23	192

juveniles, residency time of females was longer than that of males (chi-square approximation = 7.6, *d.f.* = 1, $P < .01$), but this pattern disappeared when only residents were included in the analysis (chi-square approximation = 2.2, *d.f.* = 1, $P > .10$).

Overwinter persistence of adults ranged from 30% to 75% per year for females and 35% to 67% for males (Table 5). No differences were observed between females and males within years, or for pooled data ($P > .10$). For juvenile females, 38% persisted overwinter, which was only slightly lower than that of adults (47%). Because no juvenile males were residents on the site in autumn, overwinter persistence could not be calculated.

Date of first and last captures were similar for male and female adults (mid-April to early May and mid-October to early November, respectively; Table 6). Juveniles were first captured between late June and early August. Last captures of juveniles ranged from late June to late September; these dates undoubtedly reflect disappearance of juveniles from the study area and not hibernation dates.

DISCUSSION

Relative density of thirteen-lined ground squirrels on Konza Prairie was similar to that in ungrazed prairie in Colorado (Grant 1972), but only 20-25% of that in grasslands in Wisconsin (Rongstad 1965) and grazed prairie in Colorado (Mitchell 1972). Development of a complex vertical structure of standing dead vegetation and herbaceous mulch in the absence of grazing likely had a negative impact on the abundance of thirteen-lined ground squirrels on Konza Prairie. Consistent with this idea, ground squirrels exhibited a fire-positive response, as previously noted (Beck and Vogl 1972, Finck et al. 1986, Kaufman et al. 1990b). Thirteen-lined ground squirrels prefer relatively open sites, and the removal of standing dead vegetation and plant litter by fire creates favorable habitat conditions. However, plant growth is often stimulated by spring fires (Hulbert 1986), and late in the growing season, the increased vertical structure may have a negative impact on ground squirrels.

Table 4. Median number of days (range) between first and last capture of thirteen-lined ground squirrels captured on Konza Prairie.

	Adult		*Juvenile*	
Status	*Females*	*Males*	*Females*	*Males*
Residents	60 (10-1169)	72 (8-1406)	27 (17-370)	17 (17)
n	54	50	12	1
All animals	39 (1-1169)	20 (1-1406)	2 (1-370)	1 (1-17)
n	69	75	25	23

Table 5. Overwinter persistence of resident thirteen-lined ground squirrels on Konza Prairie.

	Adult			*Juvenile*		
Years	*Females*	*Males*	*Total*	*Females*	*Males*	*Total*
1983-1984						
# in 1983	8	3	11	0	0	0
# survived to 1984	3	2	5	-	-	-
% overwintered	37.5	66.7	45.5	-	-	-
1984-1985						
# in 1984	12	13	25	1	0	1
# survived to 1985	8	5	13	0	-	0
% overwintered	66.7	38.5	52.0	0	-	0
1985-1986						
# in 1985	12	13	25	0	0	0
# survived to 1986	9	7	16	-	-	-
% overwintered	75.0	53.8	64.0	-	-	-
1986-1987						
# in 1986	20	17	37	7	0	7
# survived to 1987	6	6	12	3	-	3
% overwintered	30.0	35.3	32.4	37.5	-	37.5
Total						
Before winter	52	46	98	8	0	8
After winter	26	20	46	3	-	3
% overwintered	50.0	43.5	46.9	37.5	-	37.5

Thirteen-lined ground squirrels selected breaks with exposed limestone outcrops and rock fragments. This is consistent with general patterns reported for Konza Prairie (Finck et al. 1986). Ground squirrels also chose breaks in mid-grass and tallgrass habitats in north-central Kansas approximately 175 km west of Konza Prairie (Kaufman et al. 1990a, Kaufman and Kaufman 1989). Poorly developed soils with numerous rock fragments likely reduce the amount of herbaceous material produced and preclude development of a dense mulch layer at breaks (see Clark 1989). Use of relatively open habitats along hillsides by ground squirrels was similar to their use of moderately grazed prairie sites in Oklahoma (Phillips 1936) and high relative densities reported in grazed prairie in Colorado (Mitchell 1972).

Home range size was markedly smaller for both males (0.56 ha) and females (0.36 ha) on Konza Prairie than in other grasslands, although the trend for males to have larger home ranges than females was consistent with other studies. For example, McCarley (1966) reported that mean home range sizes for males and females were 4.74 ha and 1.42 ha, respectively. The cause of the small home range size is unknown; however, the limited distribution of preferred habitat along breaks, as well as high plant productivity in tallgrass prairie, may have reduced home range size.

Sex ratios for adult and juvenile ground squirrels were not significantly biased on Konza Prairie. These results contrast with the overall female-biased sex ratio reported by McCarley (1966). Similar numbers of male and female juveniles were captured, which was consistent with previous reports (McCarley 1966, Rongstad 1965). However, these two previous studies found a female-biased sex ratio in late summer and early autumn. We did not find a significant bias in late summer or early autumn, although the only juveniles present in autumn and captured the following spring were females. Overwinter persistence and longevity of adult ground squirrels were simi-

Table 6. Dates of first and last capture of thirteen-lined ground squirrels on Konza Prairie.

	First capture				*Last capture*			
	Adults		*Juveniles*		*Adults*		*Juveniles*	
Year	*Female*	*Male*	*Female*	*Male*	*Female*	*Male*	*Female*	*Male*
1983	3 May	2 May		20 Jul	27 Oct	28 Oct		16 Aug
1984	20 Apr	12 Apr	16 Aug		4 Nov	21 Oct	17 Aug	
1985	20 Apr	14 Mar	6 Aug		27 Oct	27 Oct	6 Aug	
1986	16 Mar	29 Mar	26 Jun	26 Jun	10 Oct	24 Oct	19 Sep	27 Jun
1987	13 Apr	21 Mar	9 Jul	9 Jul	28 Oct	28 Oct	7 Aug	7 Aug

lar between females and males on Konza Prairie. Further, dates of first emergence from hibernation in spring and last capture before hibernation in autumn of adults were within the range reported for thirteen-lined ground squirrels in Kansas (Bee et al. 1981, Choate and Fleharty 1975, Finck et al. 1986).

In summary, density of thirteen-lined ground squirrels on Konza Prairie was positively influenced by fire, likely due to removal of litter and standing dead vegetation. However, the generally low densities of ground squirrels on Konza Prairie were mostly likely related to the buildup of a deep layer of plant litter and tall standing dead vegetation caused by the absence of large grazing mammals. Our other striking result was the small home range size of the ground squirrels. The cause of this reduced home range size is unknown but may be related to the restricted distribution of preferred habitat and high plant productivity in tallgrass prairie.

ACKNOWLEDGMENTS

This is Contribution No. 92-22-A of the Kansas Agricultural Experiment Station, Kansas State University, Manhattan. Konza Prairie Research Natural Area is owned by The Nature Conservancy and maintained by the Division of Biology, Kansas State University. Research support was provided by National Science Foundation grants DEB-8012166, BSR-8307571, and BSR-8514327 and Kansas Agricultural Experiment Station project R-231 to DWK and grants-in-aid of research from Sigma Xi, American Museum of Natural History, and American Society of Mammalogists to BKC. Konza Prairie provided BKC with summer research fellowships in 1986 and 1987. We thank the many people who assisted with various aspects of this study, especially B. S. Clark, E. J. Finck, R. Fridell, M. E. Gurtz, C. Kinderknecht, and B. Willcutts. Data and supporting documentation are stored in the Konza Prairie Research Natural Area data bank (Data Set Codes = ZSM03, ZSM04, ZSM05, ZSM06, and ZSM07).

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THE DROUGHT AND POST-DROUGHT ABUNDANCE AND HABITAT DISTRIBUTION OF SMALL MAMMAL SPECIES IN BURNED AND UNBURNED, RESTORED TALLGRASS PRAIRIE

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Abstract. Drought and post-drought abundance and habitat distributions of small mammal species were monitored on burned and unburned, restored tallgrass prairie at the Knox College Biological Field Station, located in Knox County in west-central Illinois. Trap, mark, and recapture data were collected from October 1988 to March 1990. The prairie deer mouse (*Peromyscus maniculatus*), normally present in modest numbers, emerged as the dominant species during the drought and post-drought periods. Vole (*Microtus*) species, usually present in greater numbers, were absent during the drought and rare in the post-drought period. The prairie vole (*M. ochrogaster*) slowly re-established populations; the meadow vole *M. pennsylvanicus*) was scarce throughout the study. The white-footed mouse (*P. leucopus*) invaded the burned grid in low numbers in close proximity to the forest edge. The western harvest mouse (*Reithrodontomys megalotis*), extremely rare in previous studies, was absent during the drought but showed a high frequency of occurrence in the post-drought period. The continued low numbers of most of the small mammal species suggest that the effects of severe drought are long lasting. A new finding of this study indicates prairie deer mice avoid areas dominated by the allelopathic downy sunflower (*Helianthus mollis* Lam.). Adaptation to dryer conditions and absence of voles are suspected as the underlying causes of prairie deer mouse abundance.

INTRODUCTION

As part of an on-going, long-term study of small mammals in restored prairies, drought and post-drought abundance of small mammal species was monitored on burned and unburned, restored tallgrass prairie at Knox College's Biological Field Station. During the severe summer drought of 1988, prairie plants, particularly the grasses, were reduced to 25% of the height usually attained during summers of normal rainfall. Plant growth and seed production in all the grasses and some of the more shallowly rooted forbs were severely reduced although the more deeply rooted forbs, such as some of the silphiums and prairie legumes, were not significantly affected. The summer of 1989 brought increased precipitation, but the drought-affected plants returned to only 75% of their characteristic height during non-drought summers, and seed production was still negatively affected in the same species. The effects of this drought had a profound effect on the small mammal composition in this restored prairie.

The relationship between prairie habitat and the small mammals inhabiting it is dynamic, with vegetational physiognomy being a major cause of changes in species diversity, abundance, and distribution (Huntley and Inouye 1987). Precipitation has a major influence on the amount of vegetation growth and seed production (Krebs 1985). Moisture is also critical in determining the microhabitats of the prairie, which, in turn, can alter small mammal occurrence. Certain species, such as the meadow vole (*Microtus pennsylvanicus*) and shrews (*Sorex* and *Blarina*), have been shown to prefer moist conditions (Blackburn 1988, Getz 1961, Getz et al. 1987, Gottschang 1965, Synder and Best 1988). Others, like the prairie vole (*Microtus ochcrogaster*), tend to predominate in dryer areas (Getz 1961, Miller 1969, Schramm and Willcutts 1983).

Fire is also an important element in the development, maintenance, and seasonal productivity of grassland ecosystems (Anderson 1982). Fires occurred commonly during presettlement and are now used by managers to maintain the prairie community and halt the encroachment of forest, woody shrubs, and non-native herbaceous weeds. Frequent fires amplify herbage and flowering-stalk production (Hadley and Kieckhefer 1963) while decreasing litter accumulation (Hulbert 1969). Burned and unburned prairie communities contain uniquely different microhabitats. The accumulation of litter in unburned prairie forms a protective barrier at ground level that increases the relative humidity (Hulbert 1969) and provides shelter for some small mammals. The absence of litter on the burned prairie decreases topsoil moisture levels (Hulbert 1969), increases seed availability, increases exposure of small mammals to predators and environmental conditions, and leaves a litter-free understory later in the growing season (Kaufman et al. 1988). Studies have shown that voles (*Microtus* sp.) commonly inhabit areas of dense growth and litter cover (M'Closkey and Fieldwick 1975, Schramm 1970, Schramm and Willcutts 1983, Vacanti and Geluso 1985, Synder and Best 1988), but meadow jumping mice (*Zapus hudsonius*), prairie deer mice (*Peromyscus maniculatus*), and white-footed mice (*Peromyscus leucopus*) prefer more open areas with reduced litter (Schramm 1970, Schramm and Willcutts 1983, and Kaufman et al. 1988). Because of the infrequency of drought, however, no study has been able to document the effect on small mammal occurrence of extreme drought coupled with burning or litter accumulation. The purpose of this study was to investigate this effect.

MATERIALS AND METHODS

Study Area

This study was conducted from October 1988 to March 1990 at the Knox College Biological Field Station, in Knox County in west-central Illinois, on three 0.16-ha plots (grids) of restored tallgrass prairie (Figure 1). Burned Grid I was burned in March of 1987, 1988, and 1989, resulting in the absence of standing dead plants and plant litter on this plot. Intermediate Grid II was burned in March 1987 and 1988, resulting in moderate amounts of litter accumulation and standing dead plant material present on this grid during the post-drought period. Unburned Grid III had not been burned since March 1986 and contained an extremely heavy accumulation of litter and standing dead plant material at ground level throughout the study. Predominant vegetation on Burned Grid I consisted of big bluestem (*Andropogon gerardi* Vitm.), Indian grass (*Sorghastrum nutans* Nash.), yellow sweet clover (*Melilotus officinalis* Lam.), and white sweet clover (*Melilotus alba* Desr.). Intermediate Grid II was dominated by big bluestem, Indian grass, switch grass (*Panicum virgatum* L.), and downy sunflower (*Helianthus mollis* Lam.). Unburned Grid III was primarily covered by a mixture of big bluestem and Indian grass. Prairie forbs occurring on all the grids included purple and white prairie clover (*Petalostemum purpureum* Rydb. and *P. candidum* Michx.), lead plant (*Amorpha canescens* Pursh), white false indigo (*Baptisia leucantha* T. & G.), showy tick trefoil (*Desmodium canadense* DC.), round-headed bush clover (*Lespedeza capitata* Michx.), compass plant (*Silphium laciniatum* L.), prairie dock (*Silphium terebinthinaceum* Jacq.), stiff goldenrod (*Solidago rigida* L.), old field goldenrod (*Solidago nemoralis* Ait.), pale purple cone flower (*Echinacea pallida* Nutt.), wild quinine (*Parthenium integrifolium* L.), rattlesnake master (*Eryngium yuccifolium* Michx.), mountain mint (*Pycnanthemum virginianum* Dur. & Jacks.), culvers root (*Veronicastrum virginicum* Farw.), spiderwort (*Tradescantia ohiensis* Raf.), and yellow gentian (*Gentiana flavida* A. Gray).

Trapping Procedures

Each grid was a 40 by 40 meter square with Sherman live-traps placed at 10 meter intervals, resulting in 25 trapping stations per grid. Traps were set for four consecutive nights. Each trapping session consisted of four nights of trapping followed by a six night non-trapping interval. Between each session, all traps were removed. Trapping/non-trapping intervals were continual from 17 October 1988 to 5 March 1990, resulting in 32 trapping periods, for a total of 7200 trapnights. Traps were baited with commercial bird seed and checked daily. During winter months, traps were baited with one part peanut butter and one part vegetable oil combined with bird seed mix to provide additional calories for cold-weather survival. A ball of cotton for bedding was also placed in each trap. Upon capture, each animal was marked with a small, numbered, aluminum ear tag, and the following parameters were recorded: trapping period, date, tag number, grid, station number, species, sex, age, reproductive condition, weight, and any distinguishing characteristics.

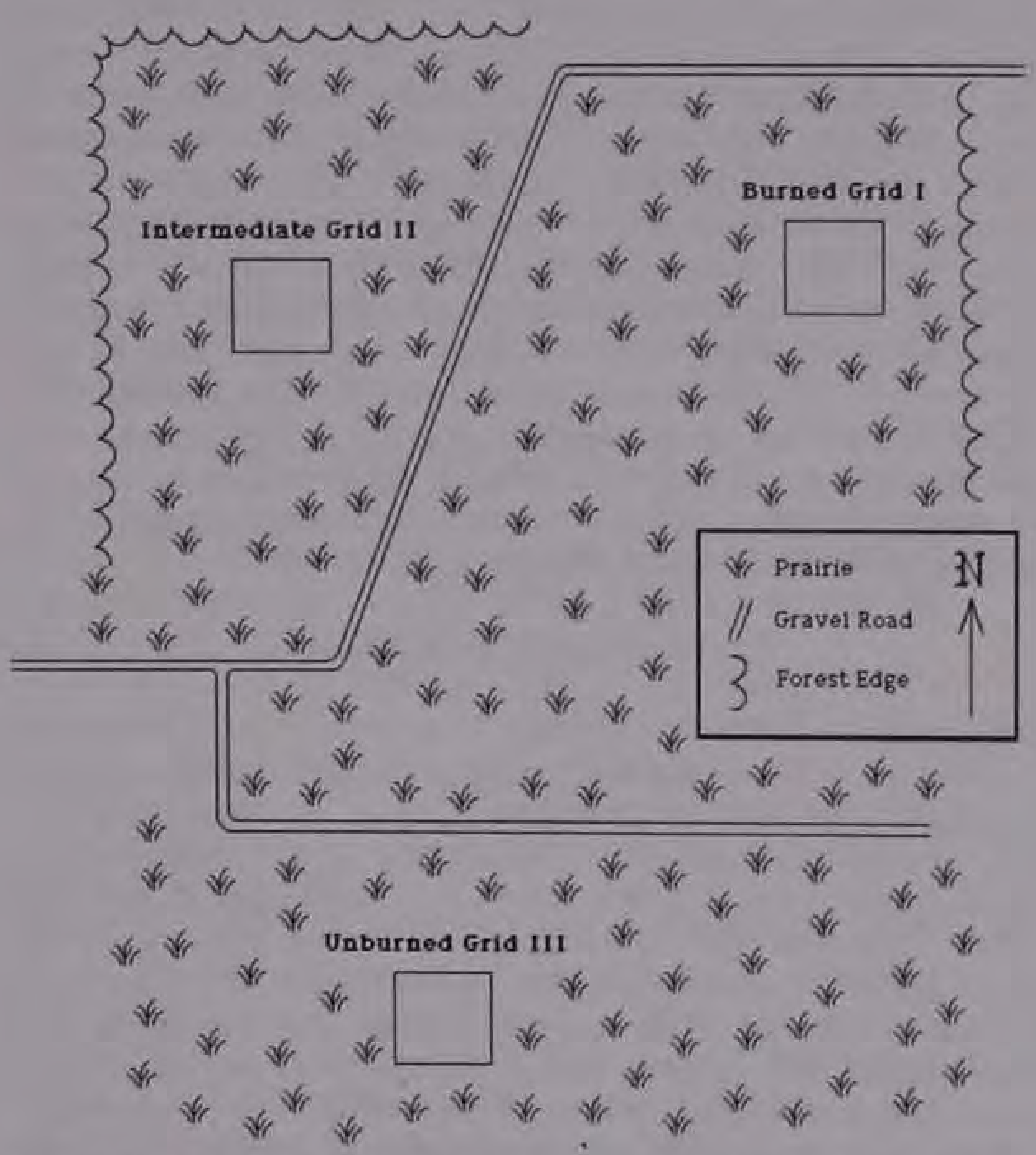

Figure 1. Map of the study area showing locations and habitats of the burned, intermediate, and unburned trapping grids.

Analysis of Data

The total number of each species in each grid was calculated. An animal was considered present or in the near vicinity in all periods between its first and last capture. Small grid size, time between recaptures, and absence of capture on theother grids of this limited habitat contributed to this conclusion. Chi-square analysis was used to determine significant differences in populations between grids and species. Pearson r and variance (R2) were also used to measure significance. Populations of individual species were measured over time.

RESULTS

Abundance and Species Composition

In this study, 301 individuals, representing nine species of small mammals, were captured 1,086 times (Table 1). The species present, in decreasing order of abundance, were prairie deer mouse (*Peromyscus maniculatus*), prairie vole (*Microtus ochrogaster*), masked shrew (*Sorex cinereus*), western harvest mouse (*Reithrodontomys megalotis*), short-tailed shrew (*Blarina brevicauda*), white-footed mouse (*Peromyscus leucopus*), house mouse (*Mus musculus*), meadow jumping mouse (*Zapus hudsonius*), and meadow vole (*Microtus pennsylvanicus*). Prairie deer mice accounted for 60.8% of the total individuals and 75.5% of the total captures. Prairie voles accounted for 11.3% of the total individuals and 4.0% of the total captures. The masked shrew accounted for 10% of the total individuals and 3.6% of the total captures. The western harvest mice accounted for 7.3% of the total individuals and 7.7% of the total captures. The remaining 10.6% of the total individuals and 9.2% of the total captures were distributed among the other 5 species encountered.

During the drought, prairie deer mice were present in significantly greater numbers on both the burned grid and the unburned grid than were other small mammal species (Figures 3 and 5). Voles, jumping mice, harvest mice, and shrews were completely absent from all grids during the drought but re-established themselves in low numbers during the post-drought period. White-footed mice were present in low numbers during the drought on the burned grid, and house mice were captured occasionally throughout the study. Prairie deer mice continued to dominate in numbers during the post-drought response on the burned and unburned grids. Prairie deer mice, along with prairie voles, harvest mice, and shrews, appeared late in the post-drought period on the intermediate grid (Figure 4). There were no marked differences in populations among any small mammal species on the intermediate grid.

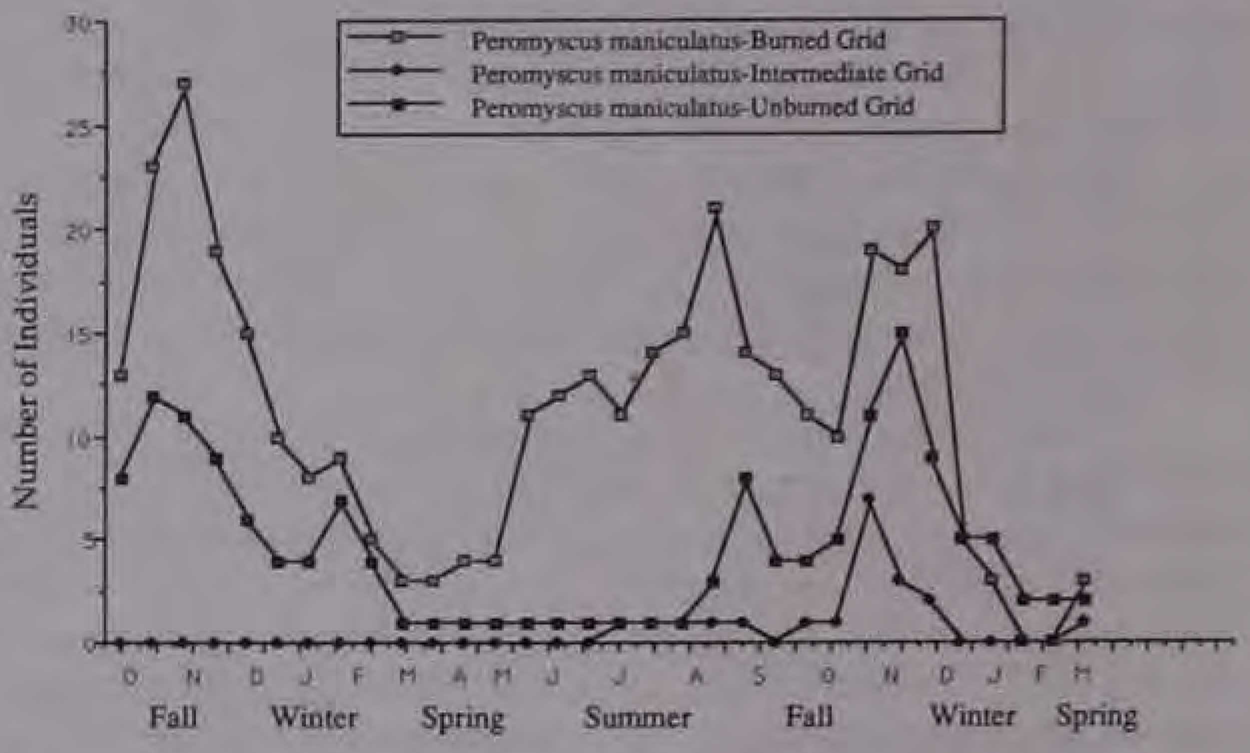

Figure 2. Comparison of *Peromyscus maniculatus* numbers on all grids through time.

Habitat Preferences and Distribution of *Peromyscus* Species

Prairie deer mice were present on all grids but occurred in the highest numbers on the burned grid (Figure 2). Populations on the burned grid were three times greater than those on the unburned grid and were significantly greater than those of the unburned and intermediate grids (X2=142.67, d.f.=2, P=<.01). Maximum population peaks occurred in late summer and fall, perhaps related to a time of maximum seed availability. No distinct differences occurred in abundance between the unburned grid and the intermediate grid (X^2=0.029, d.f.=1, P=<.01). Overall abundances of prairie deer mice declined in each grid during the post-drought period.

White-footed mice occurred only in the burned grid, primarily along the eastern boundary in close proximity to the forest edge.

Effects of the Downy Sunflower, *Helianthus mollis* Lam.

Capture points for prairie deer mice on the intermediate grid indicated a general avoidance of areas dominated by the downy sunflower (Figure 6). The two animals captured in this area were juveniles, captured late in the growing season.

Habitat Distribution of *Microtus* Species

The absence of prairie voles and meadow voles suggests significant differences in habitat preference and drought adaptability. Prairie voles were not captured until May 1989, 9 months after the severe summer drought (Figures 3 and 4). There were no significant differences between populations on any grid (X2=4.67, d.f=2, P=<.05), but a negative relationship appeared between litter accumulation and population densities, with the greatest number of prairie voles occurring on the burned grid. This species increased significantly during the post-drought period on the burned prairie (r=.6935, d.f.=12, P=<.01), moderately on the unburned prairie (r=.2191, d.f.=5, P = <.05, Figure5), and there was apparent population crash on the intermediate prairie, with numbers decreasing significantly over time (r=.6557, d.f.=15, P=<.01).

Meadow vole populations were severely reduced during the drought. There were only two meadow voles captured during the entire trapping period, both occurring 19 months after the drought. Both captures occurred on the unburned grid, where the greatest accumulation of litter was present.

Habitat Distribution of *Reithrodontomys* and Other Species

Western harvest mice were not captured during the drought, but numbers significantly increased during the post-drought period on the burned (r=-.6935, d.f.=6, P=<.05) and intermediate grids (r=.6215, d.f.=6, P=<.05, Figures 3 and 4). There were no significant differences in numbers between these grids (X2=0.0909, d.f.=2, P=<.05), but harvest mice did seem to prefer the burned and intermediate plots over the unburned plot (Figure 5).

Masked shrews and short-tailed shrews were not found during the drought but substantially increased in abundance during the post-drought period. Masked shrews first appeared 11 months after the drought summer and were present in all grids. Short-tailed shrews appeared 13 months after the drought summer but remained in very low numbers. Masked shrews outnumbered short-tailed shrews on each grid by a two to one ratio. There appeared to be a relationship between shrew populations and litter cover, with both species having the greatest densities on the unburned and intermediate grids and the lowest densities on the burned grid.

Meadow jumping mice and house mice were rare species during the study; however, house mice were caught in very low numbers on the burned and unburned grids during the drought.

DISCUSSION

The most striking effect of the severe summer drought of 1988 was the sharp reduction of total small mammal numbers and species diversity in all the habitats of the restored prairie. Past studies of the Knox College Field Station prairie in nondrought years found abundant populations of voles and shrews and the presence of jumping mice and harvest mice (Schramm 1970, Springer and Schramm 1972, Moreth and Schramm 1973, Schramm and Willcutts 1983). However, a deficit of more than 12 inches of rain in the summer of 1988 (National Oceanic and Atmospheric Administration, 1988) severely reduced the dominant prairie grass productivity and greatly altered the plant physiognomy and microhabitat, thus, changing the species of small mammals present, their numbers, and their distributions.

Effects of Drought on *Peromyscus* Species

The prairie deer mouse was the dominant species on the burned and unburned prairie during the drought. Past studies conducted on this prairie in nondrought years found modest numbers of prairie deer mice, abundant populations of voles, and the presence of as many as six other speices of small mammals (Schramm and Willcutts 1983, Moreth and Schramm 1973). However, during the extremely dry conditions of 1988, vole species, harvest mice, shrew species, and jumping mice did not occur at all on the prairie. During the drought, deer mice colonized areas and attained high densities uncharacteristic of nondrought years. Grant (1971) demonstrated that removal of voles alone could cause deer mice populations to increase. The absence of harvest mice and shrews might also play a role in the increase of deer mice numbers. Kaufman et al. (1988) found a negative relationship between high populations of deer mice and harvest mice, suggesting a possible competitive relation-

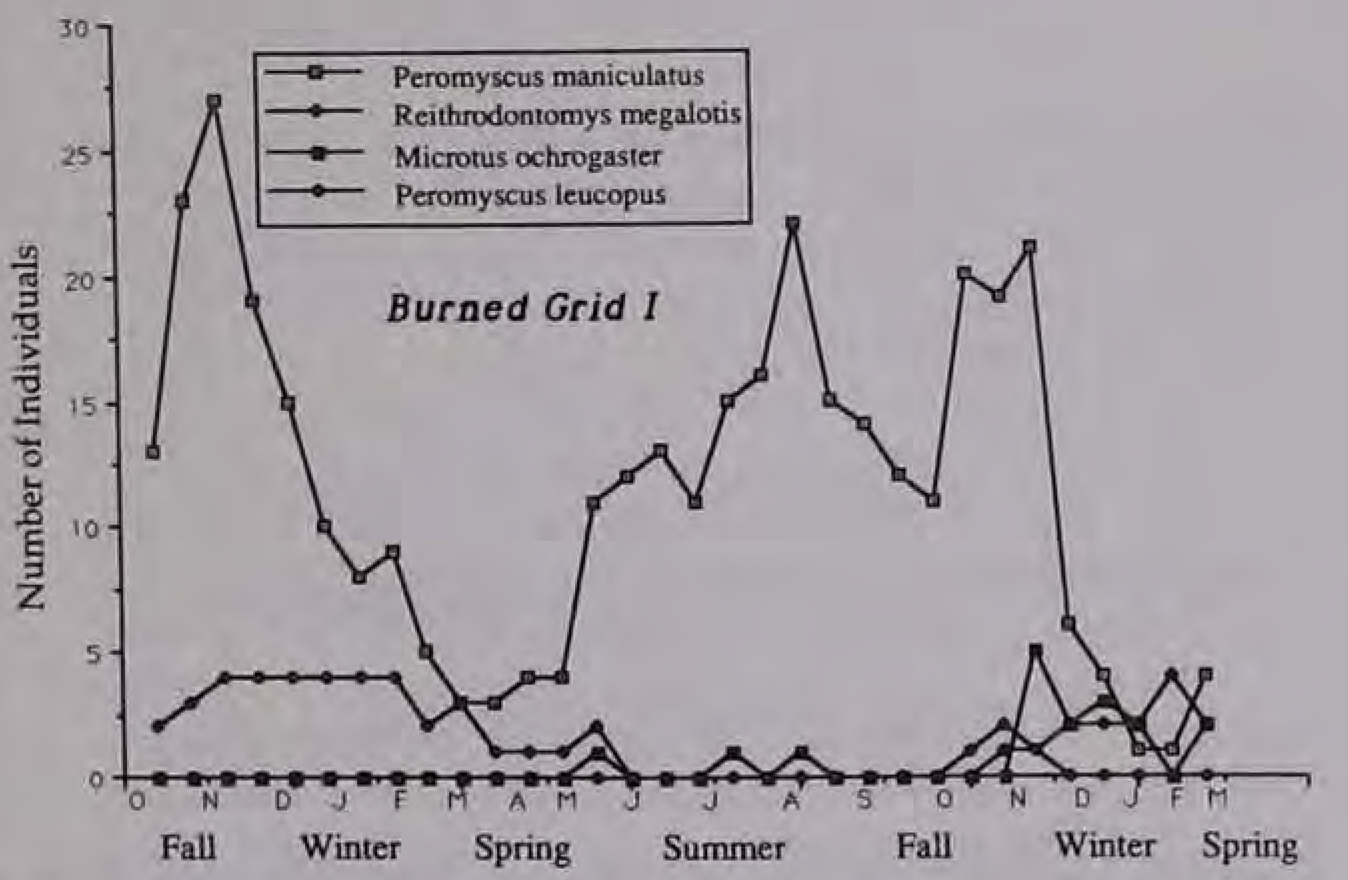

Figure 3. Comparison of mammal species numbers through time on Burned Grid I.

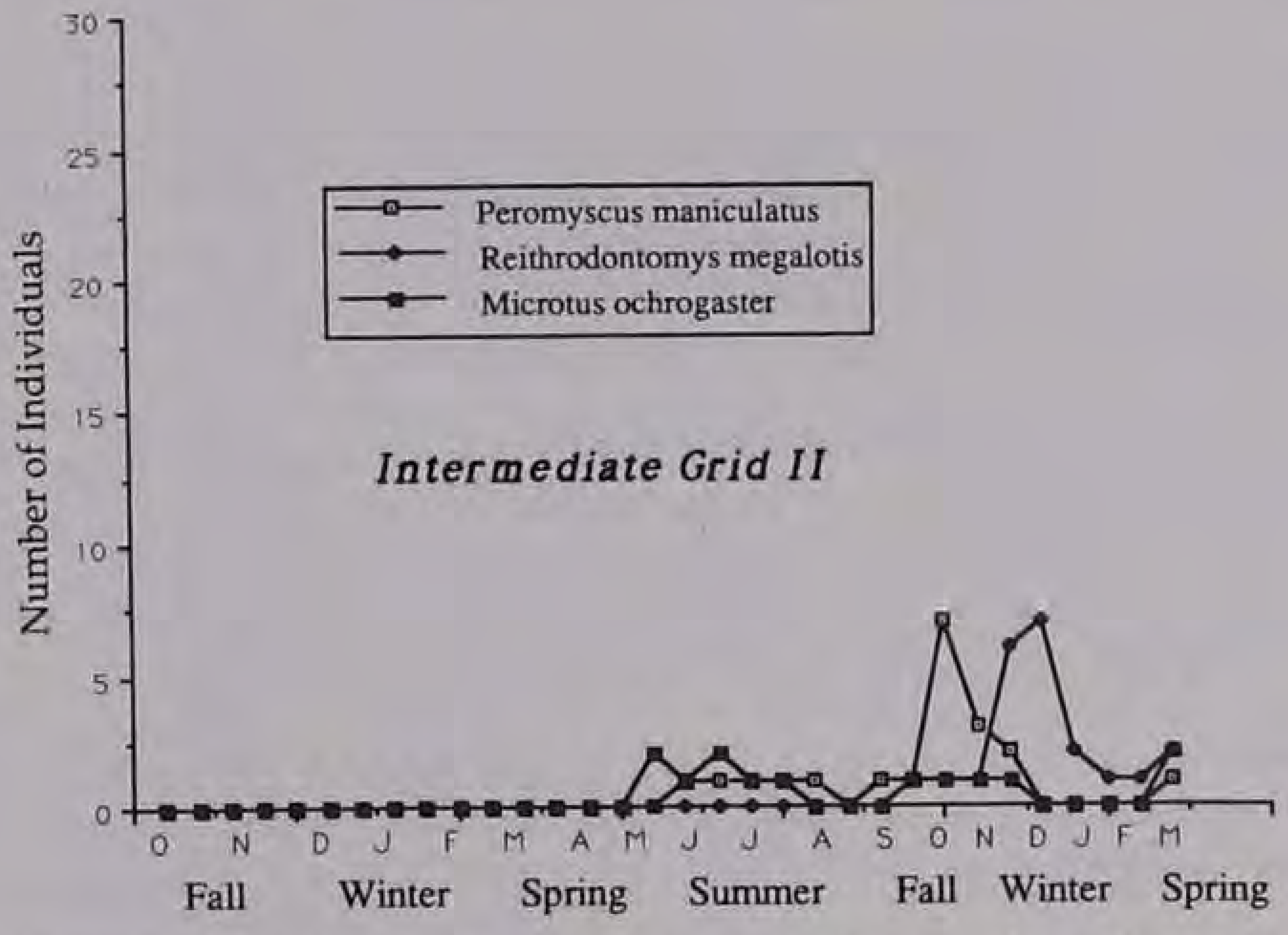

Figure 4. Comparison of mammal species numbers through time on Intermediate Grid II.

ship, but concluded habitat differences played a critical role. Short-tailed shrews have been documented as negatively affecting deer mice populations (Blackburn 1988).

That prairie deer mice have a preference for burned prairie over unburned prairie has been well documented (Schramm and Willcutts 1983, Moreth and Schramm 1973, Kaufman et al. 1988). Deer mice are primarily seed eaters and move in a series of short leaps and quick changes in direction (Gambaryan 1974). Litter accumulation on unburned prairie alters seed availability (Kaufman et al. 1988) and ease of movement, thus increasing foraging time, vulnerability to predators, and energy expenditure while moving about during above-ground activity (Schramm and Willcutts 1983). This study also found a positive association between deer mice populations and burned prairie. However, deer mice were also the dominant species on the unburned grid during all trapping periods. This differs distinctly from previous studies in this prairie during years with normal precipitation and strongly suggests that the drought, by greatly reducing the presence of other small mammal species, allowed the prairie deer mouse, in the absence of the usual interspecific competition, to colonize areas not normally used and to attain densities not possible during nondrought years.

Effects of Drought on *Microtus* Species

Vole species were completely absent during the drought and were found in reduced numbers during the post-drought period. Prairie voles were present on all grids during the post-drought period but were more prevalent in burned areas of reduced litter cover. This agrees with some studies that have shown that prairie voles prefer dry upland areas (Getz 1961) and, unlike meadow voles, can, in some years, show an affinity for burned prairie as well (Schramm and Willcutts 1983).

Meadow voles occurred very late in the post-drought period and were extremely rare. The importance of meadow voles in mesic grassland communities has been widely documented (Synder and Best 1988, Schramm 1970, Schramm and Willcutts 1983, Vacanti and Geluso 1985). Meadow voles are positively associated with heavy litter cover and very moist conditions (Getz 1961, Schramm 1970, Schramm and Willcutts 1983, Moreth and Schramm 1973, Synder and Best 1988). Miller (1969) described meadow voles as primarily lowland species, and Risser et al. (1981), described the meadow vole as an ecotonal species inhabiting the forest edge community. These findings point to the importance of moisture for this species. The effects of the drought were long lasting on meadow vole populations in the Knox prairie.

Typically, voles are slower in reestablishing populations after fire than are other small mammals. Meadow vole density is positively correlated with thickness of vegetational cover and increased litter accumulation (Vacanti and Geluso 1985). This species may take 12-16 months after a burn to repopulate areas to preburn densities (Vacanti and Geluso 1985) or may not even recover original numbers in more than 24 months (Schramm 1970). The prairie vole is more variable; Schramm and Willcutts (1983) clearly demonstrated differential response of the prairie vole compared to the meadow vole in burned and unburned prairie plots. During some years, the prairie vole can invade recently burned prairie and expand rapidly. At the same time, it may be partially excluded from adjoining unburned prairie by the presence of a lower but well-established population of meadow voles (Schramm and Willcutts 1983). In the current study, drought and fire combined to eliminate all voles on the burned grid and intermediate grid and drought alone had the same total elimination effect on both species on the unburned grid.

It should be noted that in 26 years of on-going observations and periodic trapping of voles in the restored prairies of the Knox field station, no classic, short-term, periodic, three to four year cycles have been observed, even in the less frequently burned portions of this habitat. Other recent studies in warm-season native-grass plots seem to agree on this point (Getz et al. 1987, Meserve and Klatt 1985).

Effects of Drought on *Reithrodontomys* and Other Species

One of the more unusual composition changes during the post-drought response was the relative increase in populations of the western harvest mouse. Kaufman et al. (1988) found that western harvest mice prefer areas of intermediate litter cover but will reside in both burned prairies, especially during high seed density, and unburned prairies. Western harvest mice nest above ground and may be affected by frequent fires. However, some studies show an increase in harvest mice density after fire (Vacanti and Geluso 1985). Although harvest mice are usually present in relatively low numbers (Kaufman et al. 1988), we found nearly twice the number of individuals as were found on the same prairie in nondrought years (Schramm and Willcutts, 1983). Although Kaufman et al.

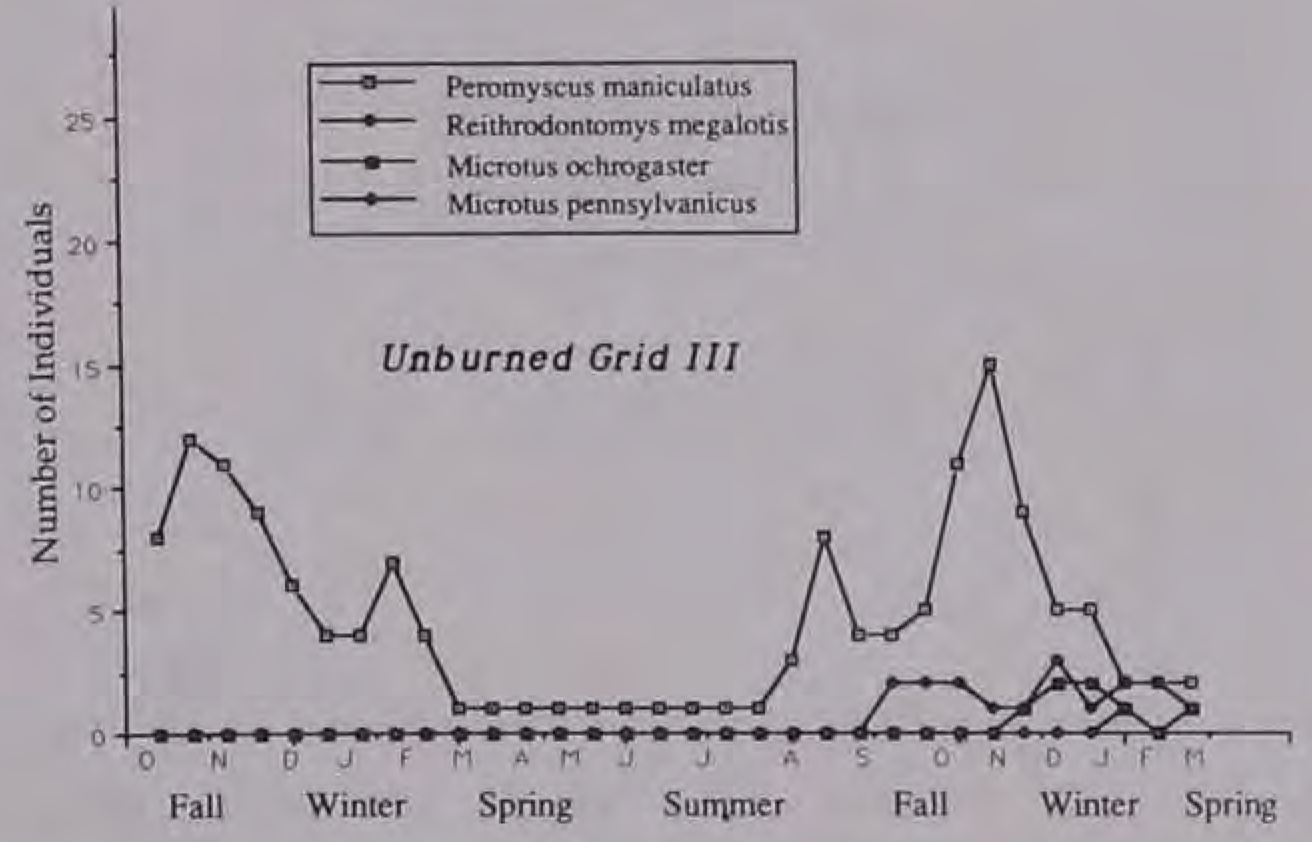

Figure 5. Comparison of mammal species numbers through time on Unburned Grid III.

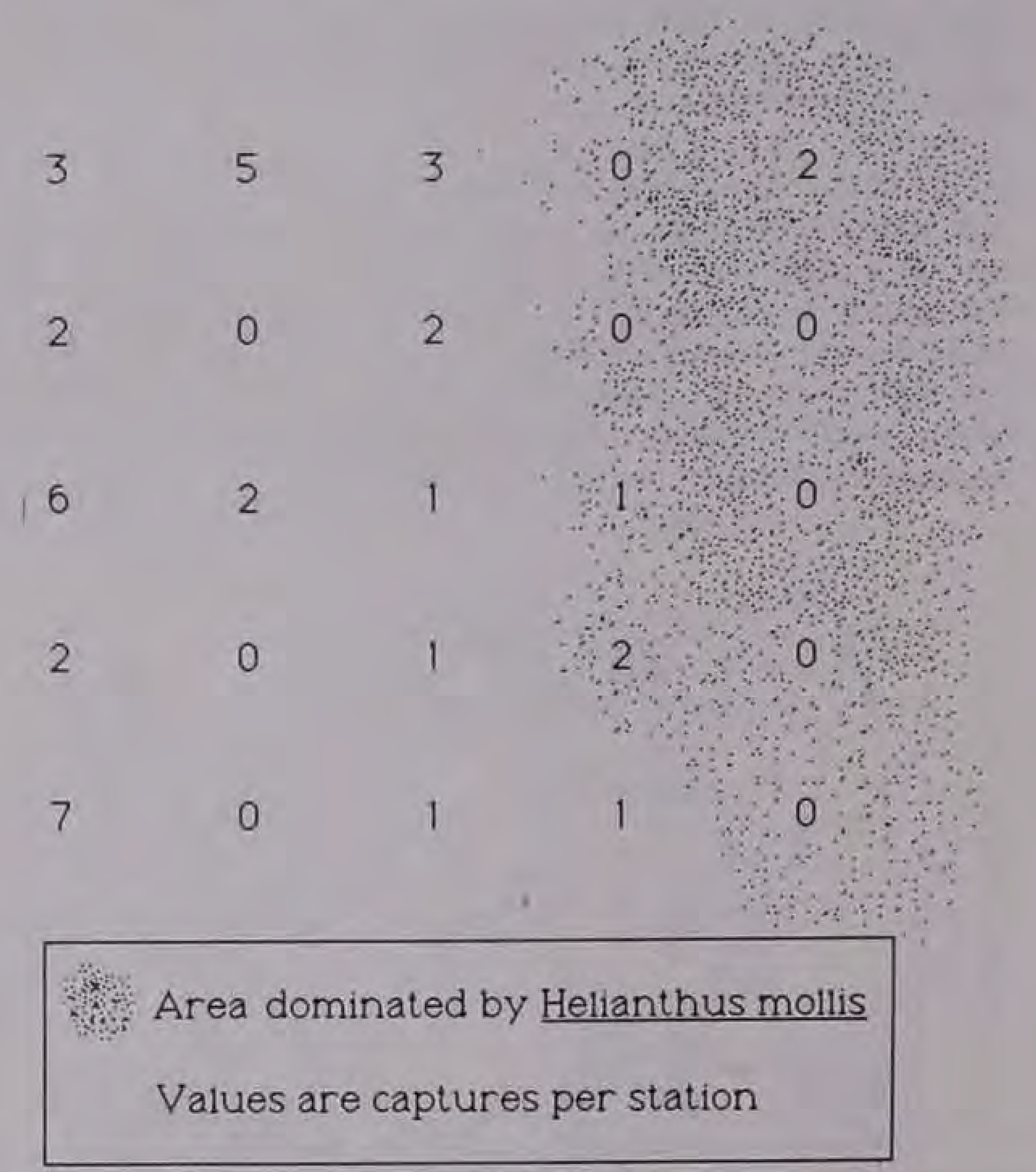

Figure 6. Captures points of *Peromyscus maniculatus* on Intermediate Grid II in relation to the allelopathic downy sunflower, *Helianthus mollis*.

Table 1. Total number of individuals for all species on each grid.

Species	*Burned Grid I*	*Intermediate Grid II*	*Unburned Grid III*	*Totals*
Peromyscus maniculatus	124	17	42	183
Microtus ochrogaster	17	10	7	34
Sorex cinereus	5	15	10	30
Reithrodontomys megalotis	7	8	7	22
Blarina brevicauda	1	7	4	12
Peromyscus leucopus	11	0	0	11
Mus musculus	2	2	1	5
Zapus hudsonius	1	1	0	2
Microtus pennsylvanicus	0	0	2	2
Totals	168	60	73	301

(1988) found a possible competitive relationship between deer mice and harvest mice, differences in habitat were cited as more important than possible interspecific competition. In our study, a more critical factor may have been the total absence of voles. Heske et al. (1984) demonstrated that interspecific competition did exist between voles and harvest mice, even though voles are primarily herbivorous and harvest mice omnivorous. The effect of the drought in eliminating the voles may have assisted harvest mice in achieving above-normal densities.

White-footed mice were found along the eastern portion of Burned Grid I. This agrees with other studies that found white-footed mice are natural forest-prairie edge dwellers and readily take to the pairie for nightly foraging (Schramm and Willcutts 1983, Clark et al. 1987, Synder and Best 1988, Kantak 1983). Although white-footed mice did increase during the post-drought period, no significant differences were found in their prairie use between drought and post-drought periods.

Shrews were absent during the drought but returned during the post-drought period. Masked and short-tailed shrews are regular residents of the tallgrass prairie (Schramm 1970, Springer and Schramm 1972, Moreth and Schramm 1973, Synder and Best 1988, Schramm and Willcutts 1983). Short-tailed shrews are recognized as a ubiquitous species, inhabiting all types of habitat, with vegetational cover having little influence on their distribution (Blackburn 1988). Masked shrews have been reported in many habitats but do not seem to be as widespread as short-tailed shrews (Blackburn 1988, Synder and Best 1988). Masked shrews increased significantly during the post-drought period, becoming the third most abundant species on the prairie. Short-tailed shrews were slower to recover and remained in low numbers. Although both species could be found in xeric habitats, they seemed to prefer more mesic sites in this study (Table 1).

Effects of Downy Sunflower on Distrbution of Prairie Deer Mice

Recent studies have focused on effects of plant chemical defenses on small mammals (Lindroth and Batzli 1986, Lindroth et al. 1986). Many plants produce phenolics in response to grazing and as a competitive defense in warding off the intrusion of other plant species. The highly allelopathic downy sunflower (*Helianthus mollis*) is found in successional stages and disturbance sites of tallgrass prairie. A stand of this sunflower is present along the eastern portion of Intermediate Grid II. During the post-drought period, captures per trap site indicated that deer mice were avoiding this area (Figure 6). The only captures in this area were two juveniles trapped late in the growing season. Lindroth et al. (1986) found that phenolics can cut the absorption of plant proteins by one half in voles but were unclear as to how this affected wild populations. The presence of this sunflower in the Knox prairies greatly reduces the presence of other prairie plants, both grasses and forbs, and this, in turn, may affect the presence of deer mice. Investigation of this phenomenon is continuing.

CONCLUSIONS

Few studies have followed the effects of severe summer drought and post-drought changes on small mammal species diversity, relative population densities, and distributions in burned and unburned prairies. During the drought, not only was plant growth greatly reduced, but small mammal populations and diversity declined as well. Both burned and unburned prairie communities were greatly affected by the drought. In the post-drought period, population density and species diversity gradually increased. Small mammal population density continued to be greater in burned areas while unburned areas with more litter cover appeared to be slower in recovering numbers and species diversity. The dominance of prairie deer mice in burned and unburned plots and the unusually high frequency of occurrence of western harvest mice suggest the importance of voles in influencing small mammal distribution and abundance in the prairie. With the reappearance of voles and shrews after the drought, the dominance by prairie deer mice appeared to be changing. Normally abundant species, such as voles, were severely affected by the drought but had started a slow recovery in numbers. Prairie voles were faster in their recovery than meadow voles, which continued to be rare. It is apparent that the effects of the drought were persisting well into the year after the drought, and the small mammal populations were still being affected residually by this phenomenon. Study is continuing as the Knox prairie recovers from the severe drought of 1988.

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FACTORS AFFECTING DICKCISSEL NESTING SUCCESS ON PARKHILL PRAIRIE

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Abstract. The reproductive success of 119 dickcissel, *Spiza americana*, nests was evaluated during a three-year study on Parkhill Prairie in northeastern Collin County, Texas. Seventy-seven clutches were lost to snake predation, five to mammals, three to brood parasitism, and one to imported fire ants, *Solenopsis invicta*. A snake trapping grid was established to identify species present and to determine their densities. During 1989 and 1990, sixty-five snakes of six species were trapped and marked, 30 were prairie kingsnakes, *Lampropeltis calligaster*. Ten marked snakes were recaptured within 15 trapping months.

INTRODUCTION

A number of avian species breed on tallgrass prairies in North America, but only two species—the eastern meadowlark *Sturnella neglecta* (Linnaeus), and the dickcissel, *Spiza americana* (Gmelin)—breed commonly on tallgrass prairies in north-central Texas. The dickcissel is characteristically more abundant, representing a relatively large amount of avian biomass, and thus interacts more frequently with other functional ecological groups.

Parkhill Prairie is a 24 ha tallgrass prairie relict in northeastern Collin County that represents one of a few such relicts remaining in north-central Texas. During a 1988 pilot study of breeding bird ecology on this prairie, I observed prairie kingsnakes *Lampropeltis calligaster* Cope, on two separate occasions, eating dickcissel eggs. Both of these instances occurred between 8:30 A.M. and 9:30 A.M. when temperatures were 80-85 F. Further, monitoring of dickcissel nests throughout the 1988 nesting season revealed high levels of snake predation during both the incubation and nestling periods.

A more detailed study was conducted during 1989 and 1990. The objectives of this study were to establish a trapping grid for snakes, to identify the species present, and to estimate their densities via mark and recapture.

METHODS

Breeding Birds

Nests were discovered primarily by dragging a rope over the vegetation while observers noted the locations from which birds were flushed (Johnson and Temple 1986). A 75 m, 20 mm diameter, nylon, braided rope was used for this purpose, with a distance of approximately 60 m between observers. Observations of breeding females revealed the locations of additional nests. Once found, each nest was marked with a numbered plastic surveyor's flag, placed 1 m north of the nest. Nests were monitored every two or three days to document the development of the young and to detect the occurence of brood parasitism and predation. Reproductive success was measured using nest-days of exposure to determine success rates for clutches monitored (Mayfield 1961, 1975).

Snake Trapping

Traps and drift fences were constructed of 6 mm hardware cloth (Milstead 1953). Exterior trap dimensions were 90 cm x 30 cm x 30 cm. Drift fences were cut to a height of 45.5 cm and buried approximately 8 cm into the sod, thus, leaving an effective height of about 38 cm. The trapping grid included four separate units, each consisting of two traps and three 7.5 m sections of drift fence (Figure 1). Each unit was oriented 90 degrees from the adjacent one, producing an "exploded box" design. The trapping grid was located in the central portion of the prairie, more than 100 m from its perimeter, in an attempt to avoid edge effect of adjacent habitats. Surrounding the prairie was cropland and overgrazed rangeland with periodic fencerows of woody vegetation.

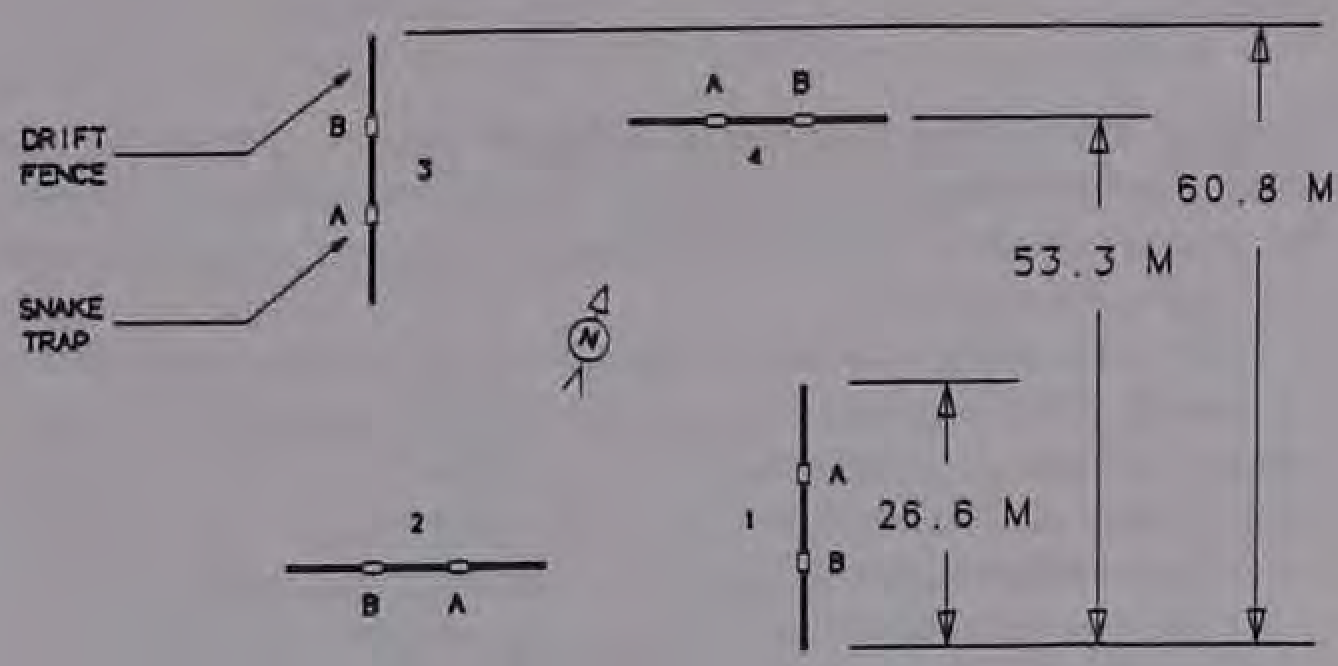

Figure 1. Parkhill Prairie snake trap configuration. Hollow rectangles indicate traps; heavy lines indicate drift fences.

Traps were monitored three times per week from May through November. Captured snakes were identified to species, measured (total body length), sexed (when possible), marked by scale clipping, and released near the location of capture. Trapping date and trap number were recorded.

RESULTS

Nesting success for incubation and nestling stages combined (n=119) ranged between 14 and 30 percent for the three-year observation period (Table 1). Table 2 illustrates the impact of various factors affecting nesting success. In the two cases where snakes were observed ingesting eggs, the eggs disappeared without structural damage to the nest itself, and no signs of egg shell remnants were present; thus, it was presumed that snakes were responsible for 77 of 86 clutches lost.

Six snake species were trapped in 1989 and 1990 (Table 3). The prairie kingsnake was the most commonly trapped, accounting for 46% of all snakes trapped. Tenant (1984) described prairie kingsnakes as more oriented toward warm-blooded prey than other kingsnakes. The relative abundance of this species and my observations of prairie kingsnakes ingesting dickcissel eggs provide more than circumstantial evidence that prairie kingsnakes are the major predator of ground nesting birds on Parkhill Prairie. Speckled kingsnakes, *L. getulus* Cope, were second in abundance, 17% of all snakes trapped, and probably also contributed significantly to dickcissel nesting losses. Indeed, the only published report of snake predation on dickcissel nests is of a speckled kingsnake reported by Facemire and Fretwell (1980). Of the remaining species captured, only the garter snake, *Thamnophis sirtalis* Garman, represents no threat to ground nesting birds, preferring cold-blooded prey (Tenant 1984). Yellowbelly racers, *Coluber constrictor* Linnaeus; coachwhips, *Masticophis flagellum* Shaw; and Texas rat snakes, *Elaphe obsoleta* Baird and Girard, all commonly include bird eggs and nestlings in their diets (Tenant 1984), but of these three species, yellowbelly racers appear to be the only species abundant enough to impact dickcissel nesting attempts. However, the remains of at least two dickcissel nestlings were retrieved from

Table 3. Parkhill Prairie snake species captured in 1989-1990.

	1989		*1990*	
Species	*No. captured*	*%*	*No. captured*	*%*
Prairie kingsnakes	12	43	19	40
Speckled kingsnakes	6	21	6	13
Yellowbelly racer	4	14	10	21
Coachwhip	3	11	1	02
Ratsnake	1	04	4	08
Garter snake	2	07	8	17

the feces of a large coachwhip. Relatively low numbers of rat snake captures may reflect their more arboreal nature, preferring the more complex vegetational strata of adjacent early and mid-seral oldfield habitats.

Collective snake activity patterns, based on number of captures per month for all species trapped (with the exception of garter snakes), indicate a general descending pattern of activity from their peak in May and June. Activity appears to remain low throughout the fall until hibernation (Figure 2). The major spring snake activity appears to coincide with the peak reproductive activity of the prairie avifauna. However, because this study focused on predation of nesting birds, snake trapping was not initated early enough to track snake activity prior to migrant breeding birds' arrival in mid-May. Platt (1988) conducted a nine-year trapping study on a Nebraska sand prairie and observed a bimodal pattern of activity in snake species (representing a different species assemblage), with peaks in the spring and fall.

Of ten previously marked snakes recaptured in 1990, eight were prairie kingsnakes, two originally marked in 1989. In addition, one speckled kingsnake and one racer were recaptured. While more information is needed on the home range size of many snake species, the high rate of recapture observed during this study (Neil Ford, University of Texas at Tyler, telephone conversation, July 1990) may indicate that at least for some species, such as the prairie kingsnake, these fragmented prairie relicts exhibit a degree of insularity.

Mammals were responsible for the loss of five clutches. In these cases, the nests were partially or completely destroyed, or they were dislodged from their original position. In addition, there were usually egg-shell fragments in the immediate vicinity. Mammals whose diets commonly include bird eggs and/or nestlings, observed or detected by the presence of tracks and/or scats in the vicinity of active nests, include nine-banded armadillo, *Dasypus novemcinctus* Linnaeus; coyote, *Canis latrans* Say; striped skunk, *Mephitis mephitis* Schreber; and raccoon, *Procyon lotor* Linnaeus. Of these species, coyotes were the most commonly observed and, therefore, are suspected for the nesting losses attributed to mammals.

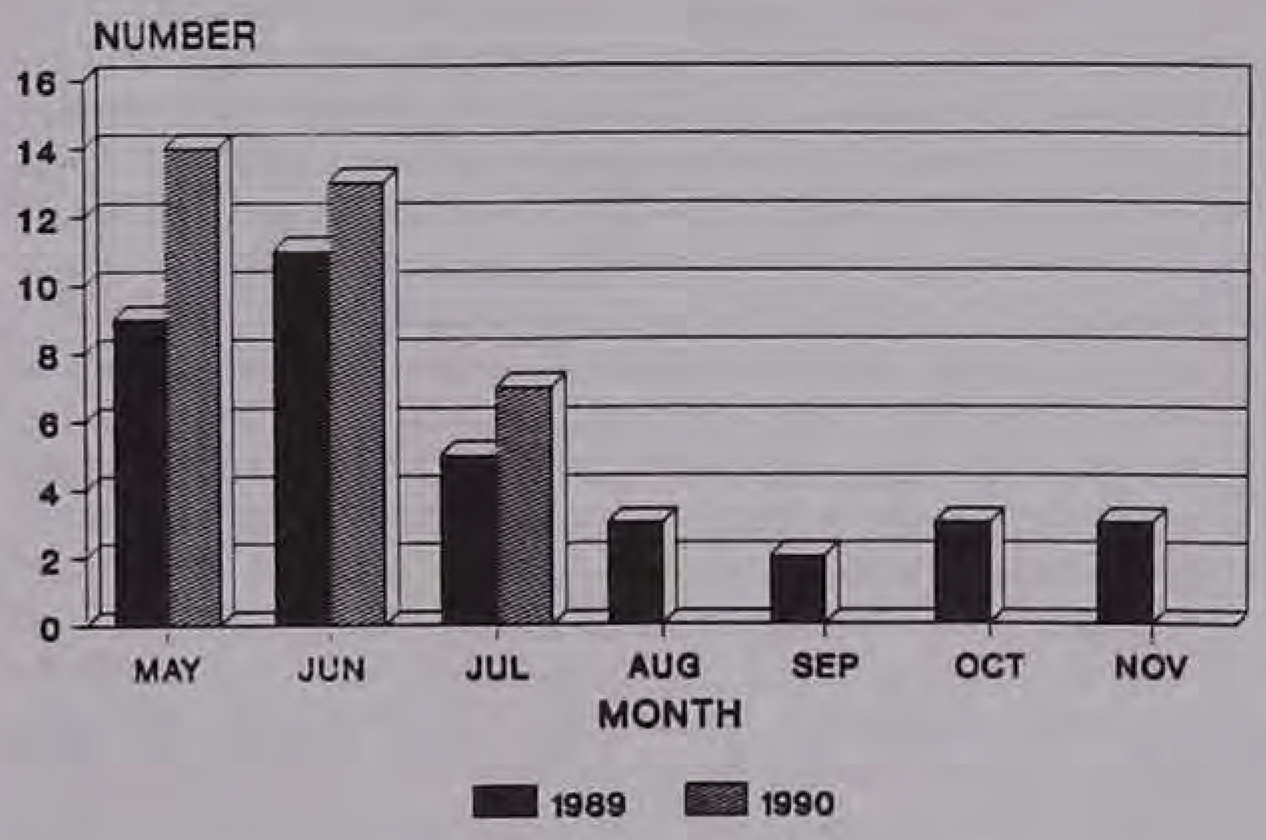

Figure 2. Collective snake species activity based on number of captures per month.

Table 1. Parkhill Prairie dickcissel nesting success, percent survival for each nesting phase (*n*=119).

Year	*Incubation*	*Nestling*	*Incubation & nestling*
1988	32	44	14
1989	44	51	22
1990	56	54	30

Table 2. Parkhill Prairie nesting failures (119 active nests).

Factor	*Clutches[1] lost*	*% of active nests*
Snakes	77	64.7
Mammals	5	4.2
Fire ants	1	0.9
Cowbird Parasitism	3	2.5
Total	86	72.3

[1] Clutches refer to eggs and/or nestlings.

Brown-headed cowbird, *Molothrus ater* (Boddaert), brood parasitism was observed in only three instances; all occurred in 1988. Of the three parasitized nests, only one survived snake predation to fledging. This pattern of relatively low brood parasitism verses high predation parallels Zimmerman's (1983) description of a similar inverse relationship between parasitism and predation observed in dickcissel populations on Kansas tallgrass prairies.

The imported fire ant, *Solenopsis invicta* Buren, was first observed to invade Parkhill Prairie in June of 1990. Data presented in Table 2 show only one clutch lost to fire ants. This observed predation by fire ants occurred when nestlings were approximately 2 days old. Nest rim height was approximately 7 cm from the ground, which was well below the mean nest rim height of 23 cm (n=41). This might suggest that an inverse relationship exists between nest rim height and fire ant predation, despite the current lack of data to support this hypothesis. Fire ants represent a new threat to ground nesting birds on Parkhill Prairie and may radically alter survival patterns in the future if they cannot be controlled.

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COMPARATIVE SPECIES DIVERSITY AND DISTRIBUTION OF BUTTERFLIES IN REMNANT AND RESTORED TALLGRASS PRAIRIE SITES

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Abstract. From 6 May to 15 October 1988, a year of severe drought, a comparative study of butterfly species diversity, abundance, and habitat distribution was conducted in restored and remnant prairies sites, both burned and unburned, in Knox, Mercer, Warren, and Henry Counties in west-central Illinois. Seasonal occurrence and selective use of and preferences for specific prairie forbs by various butterfly species were noted and compared on the various sites studied. Time of day and weather conditions were also correlated with butterfly presence and activity. Certain rare butterflies endemic to prairies, such as some of the skippers, were searched for but not found.

INTRODUCTION

Some butterflies can be found in a wide variety of habitats, others are found only in very specific habitats. Butterfly species such as the tiger swallowtail (*Pterourus glaucus* Linnaeus) and the monarch (*Danaus plexippus* Linnaeus) are found in a wide variety of habitats. Others such as the arogos skipper (*Atrytone arogos* Boisduval and LeConte) and the ottoe skipper (*Hesperia ottoe* Edwards) are endemic to the prairies. These prairie butterflies need the specific and essential food that only prairie forbs can provide for growth and reproduction (Sedman and Hess, 1985). They can therefore serve as sensitive ecological indicators, revealing the health or ills of the prairies in which they live (Tdkulsky, 1985).

Tallgrass prairies, interspersed with forests, at one time covered west-central Illinois. Due to intensive mowing and spraying of most roadways, remnant pieces of these prairies now exist primarily along railroad tracks, in nature preserves, and in a very few cases, in private hands. Only a few prairie forbs and grasses exist sporadically along west-central roads. The nature preserves are usually old cemeteries that have been left partially undisturbed for decades. Because of the loss of natural prairies, reseeded or restored prairies, such as the one at the Knox College Biological Field Station, were started in the 1950s and later.

Although there are general references to butterflies interacting with the prairie in butterfly field guides, there are few reported observations of Illinois butterflies and their plant associations. In a pioneering annotated checklist of the distribution of Illinois butterflies, Irwin and Downey (1973) referred to a general lack of records from northwest and central Illinois, except for detailed reports for Mercer and Rock Island counties in the northwest, and Peoria, Mason and Jersey counties in the center of the state. The butterflies in west-central Illinois were studied from 1975 through 1983 by Sedman and Hess (1985). Their study included more specific information on observed flight periods throughout the year, estimated number of broods, and distribution of individuals for the area. The general butterfly plant preferences for the area were also recorded. However, the counties between central, west-central, and northwest have not been studied extensively.

In this study, species diversity, abundance, and habitat distribution of butterflies, forbs, and grasses were observed in some of the northwest counties of the state. Time of day and weather conditions were also noted. Observations were made once every two weeks along a specific route through the prairies. My purpose was to analyze these observations with a sort program on a Macintosh SE/30 computer and derive the significant aspects of butterfly distribution in the prairies. They would include which butterflies are present, the flowers they prefer and some indication of the butterfly health of the prairies. Only the species and population diversity will be discussed in this paper.

METHODS

Observations

Field notes, photographs, and observations of butterflies were taken during the daylight hours for the growing season, 6 May to 15 October 1988. Butterflies were netted only when necessary, to prevent the possibility of handling effect (Morton 1984). Species, date of observation, location of capture, and any plant associations were noted. Butterflies were identified according to Irwin and Downey (1973), Pyle (1981), Scott (1986), Klots (1951), Shull (1987), and Sedman and Hess (1985). All prairie plants seen in bloom were noted even if butterflies were not present. Prairie forbs were identified according to Courtney and Zimmerman (1970), Molenbrock (1986), and Voigt and Molenbrock (no date).

Other factors noted were time of day, using a twenty-four hour clock; temperature in degrees Celsius; and the weather conditions. The weather conditions recorded included whether it was sunny, partly cloudy, or raining and whether the wind was calm, light, or strong. These factors were recorded to determine if they had any effect on the activity or diversity of the butterflies present. The location and, in some cases, the sublocations were noted.

There was no specific time table for the study; however, each location was visited at least once every two weeks. At each location, the same route of inspection was followed each time to reduce the number of variables present (Pyle 1984).

Localities

Copley Cemetery in Knox County is a 0.3 ha remnant prairie with local preservation status supported by the cemetery board and is managed by Knox College. The center of the cemetery, where the gravestones are located, was mowed, but the edges were not disturbed. This cemetery was surrounded on the west and south by a clover field and on the east by a gravel road. To the north of the site stretched a grassy waterway consisting of imported grasses. Within the cemetery were four large oak trees and a rich assemblage of prairie forbs and grasses.

Spring Grove Cemetery in Warren County is a 0.4 ha Illinois Nature Preserve. It included grasses with a few forbs. No trees were present in the slightly rolling plot, except for two small wild cherry trees. On the east side was an area of imported grasses which was mowed periodically; on the south side was a gravel road; and on the west and north sides were cornfields.

The Brownley Cemetery in Mercer County is a 0.8 ha Illinois Nature Preserve. This area is in the middle of flat farm land—the north and east sides were enclosed by cornfields; soybeans were planted on the south side; and a gravel road was on the west. This plot included both a forb-rich remnant and an adjoining three-year-old restored prairie plot. The remnant, on the north side, included mostly forbs and a few short grasses. The southern restored prairie included forbs, a few tall grasses, lambs quarters, and foxtail grass.

In Henry County, the hilly terrain of Munson Cemetery is a 1.2 ha nature preserve. This area included a rich mix of forbs and grasses with a few trees in the fence rows. The center of the area, around the graves, was mowed. Four coniferous trees were also located there. Government oats were planted on the west and north sides and corn grew on the east. To the south was a forested area of deciduous and coniferous trees separated from the cemetery by a dirt road. The Knox College Biology Field Station in Knox County included 20 ha of restored prairie surrounded by oak and hickory forests. This prairie, originally farm land, was reseeded with prairie grasses and flowers in the 1950s. It was a well-established tallgrass prairie with many of the more important prairie forbs represented. There are three sections: an east, west, and south prairie. The east prairie was close to a lake and surrounded by forest. The west and south prairies were also bordered by a forest, but were farther from the lake. They were divided by a dirt road with the south prairie being farthest from the lake. The east and west sections had been entirely burned in the spring, but the south section had not. The east and west prairies contained a wide variety forbs ranging from prairie to weedy plant species.

Data Treatment

Because of the lack of previous statistical data from other sources, our results compared to outside results can only be comparative in nature. Observations were entered into a sorting program on a Macintosh SE/30. Stat view 521 was used on data when there were enough numbers of specific butterflies observed to make any statistical data relevant.

RESULTS

Thirty different species of butterflies were captured over the season and are listed in Table 1. The common names used are from *Butterflies of West Central Illinois* (Sedman and Hess 1985).

Approximately one-third of the butterflies listed were seen only once or twice in the entire season. The skippers (Hesperidae) and Lycaenidae were almost exclusively in this group, except for the silver spotted skipper and common sooty wing. The Satyridae, Danaidae, Pieridae, Papilionidae and Nymphalidae were the most commonly occurring families throughout the study. The more common skippers were found, but rare species, such as the arogos skipper and ottoe skipper, were not seen.

Five species—common sooty wing, cabbage white, clouded sulfur, eastern tailed blue, and monarch—were observed at all sites. In a comparison of species of restored prairie versus the total of the remnant sites 20 species were common. The restored prairie had a total of 28 species while Brownley, Munson, Copley, and Spring Grove had 19,14, 14, and 10 species, respectively.

The restored prairie had the largest number of individuals, at 384. The remnant prairies of Brownley, Munson, Copley, and Spring Grove had 184, 113, 62, and 40, respectively (Table 2).

Most of the butterflies, such as the monarch, painted lady, tiger swallowtail, and silver spotted skipper, were easy to identify. However, identification for other skippers proved frustrating because of sexual dimorphism and the small physical differences among them. The differences between the clouded sulfur and the orange sulfur were apparent; however, in several cases, hybridization between the two appeared to have occurred, making identification difficult.

DISCUSSION

Previous records of butterfly distribution in Knox, Warren, and Henry counties are almost nonexistent; therefore, the presence of butterflies in surrounding counties was used as an indication of butterflies to be expected in these areas. Most habitat is the same for the areas, and the distribution of the butterflies should be the same at least for those who are strong fliers.

Table 1. Observed butterflies.

Family Papilionidae		
*	Eastern black swallowtail	*Papilio polyxenes* Fabricius
*	Yellow tiger swallowtail	*Pterourus glaucus* (Linnaeus)
Family Satyridae		
*	Little wood satyr	*Megisto cymela* (Cramer)
Family Hesperioidea		
	Broken dash	*Wallengrenia egeremet* (Scudder)
*	Checkered skipper	*Pyrgus communis* (Grote)
**	Common sooty wing	*Pholisora catullus* (Fabricius)
*	Delaware skipper	*Atrytone delaware* (Edwards)
	Dun skipper	*Euphyes vestris metacomet* (Harris)
	Hobomok skipper	*Poanes hobomok* (Harris)
	Northern cloudy wing	*Thorybes pylades* (Scudder)
	Peck's skipper	*Polites coras* (Cramer)
*	Silver-spotted skipper	*Epargyreus clarus* (Cramer)
	Southern cloudy wing	*Thorybes bathyllus* (Smith)
*	Tawny-edged skipper	*Polites themistocles* (Latreulle)
Family Pieridae		
	Checkered white	*Pontia protodice* (Boisduval and LeConte)
**	Cabbage white	*Artogeia rapae* (Linnaeus)
**	Clouded sulfur	*Colias philodice* Godart
*	Orange sulfur	*Colias eurytheme* Boisduval
Family Lycaenidae		
	Coral hairstreak	*Harkenclenus titus* (Fabricius)
	Edward's hairstreak	*Satyrium edwardsiii* (Saunders)
**	Eastern tailed blue	*Everes comyntas* (Godart)
*	Gray hairstreak	*Strymon melinus humulii* (Harris)
*	Spring azure	*Celastrina ladon* (Cramer)
Family Nymphalidae		
*	Gray comma	*Polygonia progne* (Cramer)
*	Great spangled fritillary	*Speyeria cybele* (Fabricius)
*	Painted lady	*Vanessa cardui*(Linnaeus)
*	Pearl crescent	*Phyciodes tharos* (Drury)
	Question mark	*Polygonia interrogationis* (Fabricius)
*	Red admiral	*Vanessa atalanta rubria* (Fruhstorfer)
Family Danaidae		
**	Monarch	*Danaus plexippus* (Linnaeus)

* species present in restored and at least one remnant site (20)
** species present in restored and all remnant sites (5)

When the number of species is compared to the land area, there is a correlation coefficient of 0.894, a strong relationship of area to species. This would be expected. A larger area is likely to have more habitat diversity. The Knox College Biological Field Station is not only larger, but the surrounding woodland provides more varied habitats and, therefore, increases the possibility of more species. There was also a strong correlation between total population and area (0.926) due, probably, to a larger area being more likely to have more plants and ,therefore, providing more areas for egg laying, larval food, adult perching positions and pollen for food. The quality of the area may also affect the species and population numbers but will not be handled here.

The presence of the common sooty wing, cabbage white, clouded sulfur, eastern tailed blue, and monarch in all areas was expected because they are species that use either a variety of food plants as

Table 2. Comparison by site of total population and species.

Sites	*Knox-restored*	*Brownley remnant*	*Munson remant*	*Copley remnant*	*Spring Grove remnant*	*Total remnant*	*Total All*
Size of sites	20 ha	0.8 ha	1.2 ha	0.3 ha	0.4 ha		
individuals	384	184	113	62	40	399	783
Species num	28	19	14	14	10	22	30

Correlation Coefficient population size and area 0.926
Correlation Coefficient number of species and area 0.894

adults or use plants that can be found in many different habitats. These butterflies do not need a specific rare food source and would be expected to be found.

It may be significant that 1988 was a year of severe drought and higher than normal temperatures. Rainfall for the year was twelve inches below average. There were also six days in August when the temperature was 100 degrees or above (National Climatic Data Center, 1988). The population numbers were lower compared to previous years (Sedman, personal communication). This was probably in response to the weather. While some flowers were not seriously affected, others were, and the grasses that usually grow six to seven feet tall were no taller than two feet by the end of the season. This difference in vegetation may have also been a contributing factor to the absence of butterfly species and numbers.

Other butterflies, such as the skippers, need specific plants for adult egg laying, perching positions, pollen for food and larval food. Plant species present in an area can be indicators of potential butterfly presence. Some of the larval food plants, usually grasses, of the skippers have not been studied thoroughly, and little is know of skippers nutritional needs or specific preferences in this area. Since the same assortment of prairie grasses was found in all areas one would expect the ottoe skipper and possibly the arogos skipper to be present in these areas. However, they were not. In southwest Minnesota, Dana (1989) found the ottoe skipper in association with big bluestem (*Andropogon gerardii*), little bluestem (*Andropogon scoparius*), and pale purple coneflower (*Echinacea pallida*). Sedman and Hess (1985) found the ottoe skipper associated with little and big bluestem and purple coneflower (*Echinacea purpurea*) but did not know the larval food plant for their area. Although little and big bluestem were found in all areas observed, along with the pale purple coneflower (*Echinacea pallida*). Sedman and Hess (1985) also found the agoros skipper associated with little and big bluestem grasses and purple coneflowers. Although little and big bluestem were found in all areas observed, along with the pale purple coneflower, these two skippers were not found. The difference in coneflower species may be a factor in the absence of the butterflies. More study needs to be done with prairie butterflies in these areas.

Behaviorally, skippers tend to not travel far from the areas where they live; therefore, they would be very susceptible to local extirpation under extreme conditions. They also tend to be colonial and are not spread out evenly over an area (Sedman and Hess, 1985). It may be that these species never inhabited the study sites, but Sedman and Hess (1985) found the rare prairie species in their study. The rare skippers may have been at the remnant sites but were just not observed. The skippers would not be expected in the restored prairie because of their colonial tendencies and the absence of any close remnant prairie that might act as a butterfly source.

The detailed history of these sites is not known. All are surrounded by farm land that in the past may have been sprayed with pesticides, thus, adversely affecting the populations. Some of the sites had been mowed intermittently. All sites have been burned intensively for several successive years to promote forb and grass growth and to stunt or kill exotics. While ottoe skippers do overwinter underground (Dana, 1989), late spring burns with low fuel or high fuel fires in early spring may kill larvae. The ottoe skipper has been known to survive partial burning in Illinois prairies (Panzer, 1988). In the absence of conclusive evidence regarding the effects of prairie burns on butterfly life history stages, a concern for the survival of these prairie insects dictates burning no more than half of a remnant in any given year.

Invertebrate inventories need to be done on areas that have been infrequently burned to observe whether and which rarer species are present to help in the formulation of a more nearly optimum burn program for both flora and fauna.

ACKNOWLEDGEMENTS

This study was supported by a Ford Foundation grant. Knox College provided the computer time.

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B.A Seger

DIVERSITY OF WANDERING SPIDERS (ARANEAE) COLLECTED BY PITFALL TRAPS IN NORTHERN ILLINOIS PRAIRIES AND WOODLANDS

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Abstract. Spiders were collected by pitfall traps in various natural communities in northern Illinois: a young prairie restoration, a relatively high-quality prairie, a high-quality savanna, a degraded savanna woodland, and a degraded woodland forest. Diversity of the wandering or cursorial spiders was highest for the older, less-disturbed communities—the quality prairie and savanna and the woodland forest. The two woodland sites showed strong community similarity, as did the two prairies. The savanna showed weak similarity to all of the other four sites. Clubionidae were important in woodland areas; Lycosidae were dominant in the prairies and savanna.

INTRODUCTION

Invertebrates, including spiders, play critical, though poorly understood, roles in natural communities. Spiders are a dominant group of predators in terrestrial habitats, achieving high populations in most communities. Distinct spider faunas are characteristic of specific plant associations (Muma 1973). Although some are specialists, spiders are often generalist feeders. In this role, their diversity influences community structure, and, probably, increased spider diversity leads to increased diversity of other taxa. In spite of this, spiders in prairies and savannas have been very little studied (Wolff 1990).

Pitfall trapping is an efficient method of sampling the active invertebrates, primarily arthropods, on the soil surface (Uetz and Unzicker 1976). This study examined the diversity of wandering or cursorial spiders in several communities representative of natural areas in northern Illinois. Specific goals were to determine the spider fauna present in these natural areas, to determine the diversity of these communities, and to examine the community similarity along a prairie-savanna-woodland gradient.

METHODS

This study was conducted by pitfall trapping with 10 simple cup traps for each transect. A 1:1 mixture of ethylene glycol and water was used as an entrapping and killing fluid. Different time periods were used before emptying traps, but each transect was trapped through the summer months. Some traps were disturbed by animals, probably raccoons or skunks. Data from the traps were lumped, and overall numbers from each transect were sufficient for analysis.

The five study areas constitute a prairie-savanna-woodland gradient, including two prairies, a savanna, a savanna woodland and a woodland forest. The Morton Arboretum Prairie is slightly more than 2 acres of restored mesic tallgrass prairie with a high diversity of planted grasses and forbs. The Morton Arboretum Meadow, an area adjacent to the prairie restoration and containing some relatively undisturbed portions, was last plowed in 1961. It is a high-quality native prairie dominated by Indian grass and big bluestem, but it is low in forb diversity. It has been burned annually during the previous ten years.

Middlefork Savanna is a 10-ha tract of relatively high-quality, somewhat disturbed savanna. Large burr and white oaks provide an open canopy with a diverse grass and herbaceous ground flora characteristic of savannas. Reed-Turner Woodland Preserve is a 15-ha woodland that was historically a more open savanna. It is now a closed-canopy, dry-mesic to mesic woodland with burr, white, black, and red oaks, as well as hickory trees, but with an apparent loss of plant diversity. Morton Arboretum Woods is an extensive woodland that has grown into a closed-canopy forest. Dominated by maple and various oak trees, the forest is typical of many in the area, altered by grazing and fire suppression.

Diversity indices and community similarity analyses were conducted by standard methods as described in Magurran (1988) and Brower et al. (1990)

RESULTS AND DISCUSSION

Distinct patterns are seen in the analysis of diversity in the five habitats. Table 1 lists the spider species identified and their numbers. In Table 2, the diversity indices are calculated. Morton Arboretum Meadow prairie had the highest species diversity or richness, with 21 species of wandering spiders. Middlefork Savanna and Morton Arboretum Woods each had relatively high species diversity, with 17 species each. The Morton Arboretum Prairie restoration has the lower diversity of 14, possibly because of its small size and youth. Reed-Turner Woodland, probably suffered the greatest community structure change, from savanna to closed woodland, and had the least diversity, only 11 species.

Sac spiders of the family Clubionidae showed a greater dominance in the two woodland areas; wolf spiders of the family Lycosidae were dominant in the prairie areas and in the savanna. Crab spiders of the family Thomisidae were relatively common, with one species of *Xysticus* abundant in the prairies and a different species common in the woodlands.

Diversity indices sensitive to richness (Table 2), such as Margalef, showed a clear pattern with Morton Arboretum Meadow being the most diverse followed by Middlfork Savanna and Morton Arboretum Woods. The Menhinick index (Table 2), which is affected by the number of specimens, had Middlefork Savanna highest, followed by Reed-Turner, Morton Arboretum woods, then the Meadow, with the restored prairie scoring rather low.

The evenness index of Pielou and the heterogeneity index of Simpson (Table 2) both showed the Morton and Reed-Turner woods to be most diverse, with the Meadow and Savanna following. Shannon, considered by Bultman et al. (1982) to be the best index for pitfall studies, showed the Morton Arboretum Woods to be the most diverse, followed by the Meadow, Reed-Turner, and the Middlefork Savanna close together, and the restored prairie with low diversity. Overall, the communities that were less disturbed, older, or with fairly large tracts had higher diversity as indicated by these indices. Demonstrating the importance of diversity measures for distinguishing native communities is difficult because of the different components used in evaluating data. Although the indices basically agreed with perceptions of the communities, more extensive sampling should allow for precise evaluation of communities using spider diversity.

Community similarity indices, such as the Jaccard Coefficient (Table 3) and Percent Similarity (Table 4), demonstrate that the

Table 1. Number and species of spiders trapped in each of the five study areas.

	Number trapped				
Species	*RTW*	*MFS*	*MAM*	*MAP*	*MAW*
Anyphaenidae					
Anyphaena pectorosa					5
Clubionidae					
Agroeca ornata	7				
Agroeca pratensis	1				
Castianeira cingulata	2				23
Castianeira descripta			1		
Castianeira longipalpa					1
Castianeira trilineata		1			1
Castianeira variata			1	2	
Clubiona kastoni	1				2
Phrurotimpus alarius	8				37
Phrurotimpus dulcineus			3		
Scotinella fratella					1
Scotinella madisonia			6		
Gnaphosidae					
Drassyllus depressus			8	6	
Drassylus sp.			1		
Gnaphosa parvula		1			
Haplodrassus signifer				1	
Herpyllus eclesiasticus	1				2
Micaria pulicaria		1			
Sergiolus decoratus			2	1	
Hahniidae					
Neoantistea agilis			1	2	
Neoantistea sp.		1			
Pisauridae					
Dolomedes sp.					2
Lycosidae					
Allocosa funerea		4			
Arctosa rubicunda			2	3	
Hogna helluo			2		
Pardosa milvina		4			
Pardosa moesta		10			
Pardosa saxatilis		10	126	204	
Pirata insularis		3			
Pirata minutus	1	63	3		1
Pirata sedentarius		1			
Schizocosa avida			6	3	
Schizocosa bilineata			17	9	1
Schizocosa crassipalpita		1			
Schizocosa ocreata	6	8			32
Schizocosa retrorsa			23	1	
Trabeops aurantiaca	5	1			
Trochosa pratensis					1
Trochosa terricola		4			
Philodromidae					
Thanatus rubicellus			4	1	
Thomisidae					
Ozyptila conspurcata				1	
Ozyptila georgiana			2		
Ozyptila sincera canadensis					7
Xysticus ferox					5
Xysticus fraternus	29				27
Xysticus triguttatus			32	34	
Salticidae					
Evarcha hoyi		1			
Habrocestum pulex	2		2		5
Phidippus pius		1	1	1	
Sitticus cursor			4		

RTW = Reed-Turner Woodland; MFS = Middlefork Savanna; MAM = Morton Arboretum Meadow; MAP = Morton Arboretum Prairie restoration; MAW = Morton Arboretum Woods.

Table 2. Diversity indices for communities listed in Table 1.

	Community				
Index	*RTW*	*MFS*	*MAM*	*MAP*	*MAW*
Individual Richness (n)	63	115	247	269	153
Richness					
Species (s)	11	17	21	14	17
Margalef	2.41	3.37	3.63	2.32	3.18
Menhinick	1.39	1.59	1.34	.85	1.37
Heterogeneity					
Simpson	.75	.68	.71	.41	.84
Shannon (H')	1.77	1.76	1.85	.97	2.11
Evenness					
Pielou	.74	.62	.61	.37	.74

Table 3. A community similarity index, the Jaccard Coefficient of Community, comparing the communities in Table 1.

	RTW	*MFS*	*MAM*	*MAP*
MFS	.120			
MAM	.067	.086		
MAP	.000	.069	.522	
MAW	.400	.097	.086	.033

Table 4. A community similarity index, Percent Similarity, comparing the communities in Table 1.

	RTW	*MFS*	*MAM*	*MAP*
MFS	9.4			
MAM	2.0	10.3		
MAP	0.0	9.1	73.4	
MAW	49.5	8.3	2.1	.65

Morton Arboretum Meadow prairie and Prairie are rather similar, as are the Reed-Turner and Morton Woods. All other similarity figures were low, although Middlefork Savanna did show some weak similarity to each of the other communities. This suggests the possibility that the savanna is a community distinct from prairie or woodland, based on soil surface and cursorial spiders.

Dominance-diversity curves, which are also known as relative abundance curves or rank abundance plots (Magurran 1988), are presented for Middlefork Savanna (Figure 1) and for the Morton Arboretum Meadow (Figure 2). These curves demonstrate that the communities are approaching a log normal distribution, which is characteristic of natural communities.

The diversity and similarity analyses indicate that the spiders from prairie, savanna, and woodland are faunally separate communities, are rather diverse if the community is relatively undisturbed, and have characteristics of natural communities. More extensive studies need to be done to confirm and expand the findings reported here.

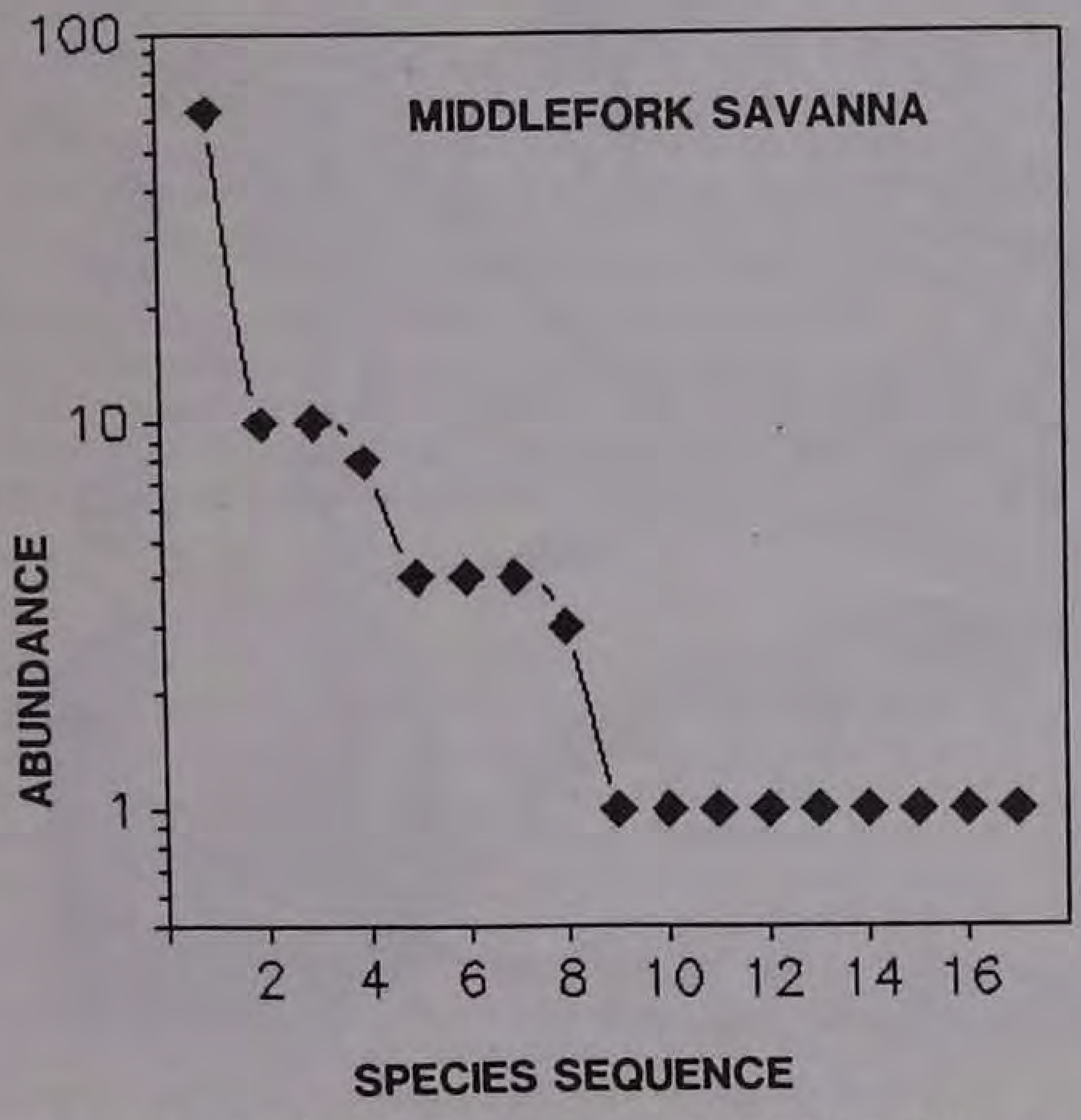

Figure 1. A dominance-diversity curve for Middlefork Savanna.

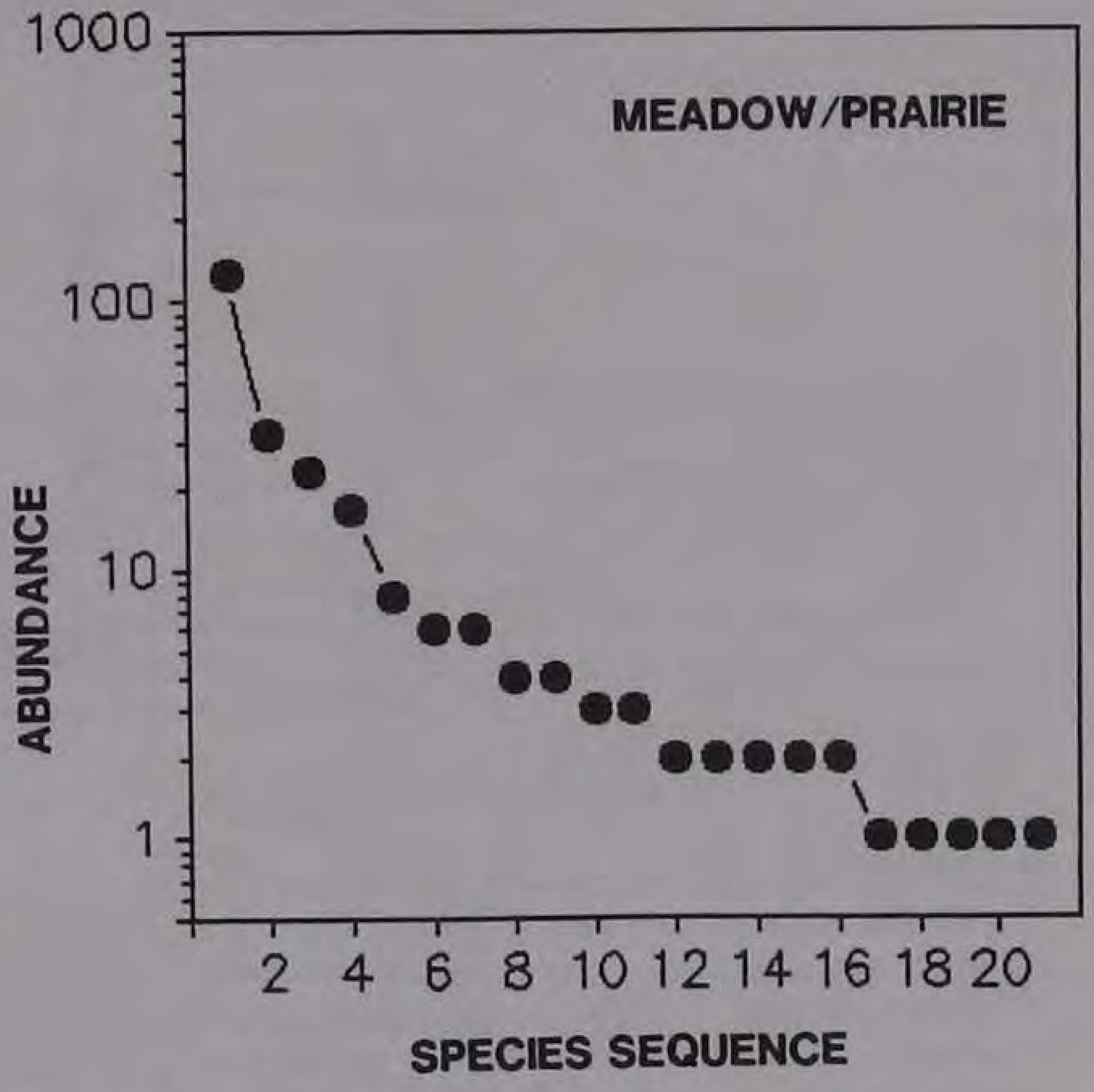

Figure 2. A dominance-diversity curve for the Morton Arboretum Meadow prairie.

ACKNOWLEDGEMENTS

Morton Arboretum funded the research conducted on their grounds. Dr. Gerould Wilhelm and Dr. George Ware encouraged study of the spiders of natural areas. The Illinois Department of Conservation Nongame Wildlife Conservation Fund provided funds to Applied Ecological Services to study Middlefork Savanna and Reed-Turner Woodland. Steve Apfelbaum encouraged our participation. Joyce Keesy, Gia DiMartinis, and Dan Applegate conducted field work and the initial sorting. Deep thanks to all of the above.

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ANTS OF A NORTHERN ILLINOIS SAVANNA AND DEGRADED SAVANNA WOODLAND

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Abstract. In this first attempt to determine the ants inhabiting savannas of North America, pitfall trap collections of ants from a high-quality, black-soil savanna were compared to those from a degraded savanna that has become a woodland: Middlefork Savanna and Reed-Turner Woodland in Lake County in far northeastern Illinois. More than 20 species were identified from the savanna and 16 from the woodland. In terms of numbers of times collected, *Formica* was dominant in the savannah, with *Lasius* and *Myrmica* next, followed by *Camponotus*. The woodland collections were dominated by *Myrmica*, followed by *Camponotus* and *Lasius*. A minimum of 40% of the species were shared by the two habitats. Middlefork Savanna had higher diversity in all indices used to evaluate diversity, including those accounting for species richness, numbers of individuals, heterogeneity, and evenness. Transects within the natural communities had a higher Quotient of Similarity than did comparison of the communities.

INTRODUCTION

Ants are among the most important faunal members of terrestrial communities, having a high species richness and often the highest biomass. Members of the Order Hymenoptera, Family Formicidae, ants are social insects able to form large colonies. Ants have a substantial impact on their habitats. Holldobler and Wilson (1990) report that ants move at least as much soil as earthworms and, in many cases, signifcantly more. Because native North American earthworms are absent from the northern prairie areas (Gates 1970), and probably from northern savannas as well, ants are the dominant soil movers in these habitats.

Ants affect plant distribution and survival by eating seeds, dispersing seeds, or manipulating seeds to allow germination. They also affect the presence of other organisms, such as beetles and spiders (Holldobler and Wilson 1990). The structure or composition of the community and any disturbance within that community will influence the ant species present and the total ant diversity. Many ant species are, thus, good indicator species of natural areas.

In order to understand, manage, and restore natural areas, it is critical to understand the ants that should be present and their biology. This study is the first attempt to determine which ants occur in savannas of the prairie regions of North America.

METHODS

In 1986 and 1987, pitfall trapping was conducted by Joyce Keesy of the Department of Entomology, University of Wisconsin, as part of a larger study by Applied Ecological Services (Keesy 1988). The ant specimens were sent to our lab. The two sites trapped are located in Lake County in the northeastern corner of Illinois. Middlefork Savanna (MFS) is a 10-ha high-quality, black-soil, open savanna. The Reed-Turner Nature Preserve (RTW) is a closed, oak woodland, degraded from its former open state. For each year, two transects of 10 traps each were placed at MFS, and four transects of 10 traps each were placed at RTW. Five, 24-hour sampling periods were conducted each year during the months of June, July, and August.

Analyses of the data to determine diversity and community similarity were conducted by standard methods as detailed in Magurran (1988) and Brower et al. (1990).

RESULTS AND DISCUSSION

The ants identified from the savanna and degraded savanna-woodland sites are listed in Table 1. Twenty-six species were identified from the collections although some of these were only identified to genus because of taxonomic problems or the lack of a reliable revision of the group. For ants from each set of samples, species richness varied from nine species in one transect of the degraded woodland to 20 species in the high-quality savanna transect.

Results from two transects in Middlefork Savanna differed strongly (Table 1). This was because transect 1 was very close to standing water and the ant fauna was affected. Transect 2, located through the middle of a typical savanna habitat, showed clearly higher diversity (Table 2). The transects in the degraded woodland were similar to each other in species richness and the species present. In terms of numbers of times collected, *Formica* was dominant in the savannah, with *Lasius* and *Myrmica* next, followed by *Camponotus*. The Woodland collections were dominated by *Myrmica*, followed by *Camponotus* and *Lasius*. A minimum of 40% of the species were shared by the two habitats.

The following discussion compares savanna transect 2, the higher-quality area, with the woodland transects, including the analysis of the lumped data from the four woodland transects. Using DuBois' (1989) list of ants that occur in Illinois prairies, we found that of the 15 species listed for prairies in the study area, six occurred in the savanna. In contrast, the woodland sites had only four species listed as prairie ants. This overlap of prairie species in the savanna is expected, but more data is needed to clearly delineate a savanna ant fauna and the species it shares with prairies.

Diversity indices which incorporate species richness and number of individuals, such as Margalef and Menhinick, show the Middlefork Savanna transect with 20 species to have a much higher diversity than the woodland transects with 10 to 12 species (Table 2). However, even the savanna diversity of 20 species would be considered low for a native prairie according to Trager (1990), but the lower number may be due in part to limiting collecting to one method, pitfalls.

Diversity indices that account for heterogeneity, Simpson and Shannon (H'), and an index of evenness, Pielou, all indicated that the savanna transect had higher diversity than the woodland. The stable savanna area was more diverse by all measures. Diversity appears to have been reduced in the woodland by it's degradation from it's former, more open, savannalike condition.

Using the Quotient of Similarity (Table 3), the woodland sites are very similar to each other. The transects vary from 73% to 80% similarity among themselves and range from 77% to 86% when

Table 1. List of all ant species found in Middlefork Savanna and Reed-Turner Woodland during study.

		Transects							
Species	*Prairie* [b]	*WTOT*	*STOT*	*MFS1*	*MFS2*	*RTW1*	*RTW3*	*RTW5*	*RTW8*
Ponerinae									
Amblypone pallipes		1				1			
Ponera pennsylvanica	C		1		1				
Myrmicinae									
Aphaenogaster rudis		5					5		
Crematogaster cerasi		2	1	1					
Crematogaster punctulata	O								
Leptothorax curvispinosus [a]		2	14	3	11	1	1		
Leptothorax schaumi		1	1		1			1	
Monomorium minimum	C								
Myrmecina americana		16				1	6	3	6
Myrmica americana	O		124	16	108				
Myrmica emeryana			6	1	5				
Myrmica lobicornis fracticornis			6	2	4				
Myrmica spp. [a]		696	59	4	55	170	152	257	117
Solenopsis molesta [a]	C								
Stenamma brevicorne		8	1		1	1	2	5	
Stenamma diecki		1					1		
Stenamma impar [a]		6				2	1		3
Stenamma schmittii		14	7	2	5	9		1	4
Tetramorium caespitum [a]			7	4	3				
Dolichoderinae									
Dolichoderus pustulatus	R								
Tapinoma sessile	C	11	5		5		3	5	3
Formicinae									
Acanthomyops claviger	O								
Acanthomyops interjectus	O								
Acanthomyops latipes	R								
Camponotus novaeboracensis			1		1				
Camponotus pensylvanicus		449	37	3	34	87	307	36	19
Camponotus caryae caryae			6		6				
Formica spp. [a]	10 spp	43	489	380	109	3	17	19	4
Lasius alienus [a]		215	212	23	189	50	84	52	29
Lasius flavus			3		3				
Lasius neoniger	C		4		4				
Lasius speculiventris		1							1
Polyergus breviceps	O								
Polyergus lucidus	O								
Prenolepis imparis	C	127	53		53	37	17	52	21

Transects: MFS1, MFS2 from Middlefork Savanna; TOTS the total of the two savanna transects; RTW1 through RTW8 from Reed-Turner Woodland; TOTW the total of all woodland transects.

[a] True prarie species (Gregg 1944).

[b] Those species believed to occur in prairies (DuBois 1990): C = common; O = occasional; R = rare.

Table 2. Diversity indices for transects listed in Table 1.

	Transects							
Index	*TOTW*	*TOTS*	*MFS1*	*MFS2*	*RTW1*	*RTW3*	*RTW5*	*RTW8*
Individual Richness (N)	1596	1038	439	599	362	596	431	207
Richness								
Species (s)	16	20	11	20	11	12	10	10
Margelef	2.03	2.74	1.64	2.97	1.70	1.72	1.48	1.69
Menhinick	.40	.62	.53	.82	.69	.49	.48	.70
Heterogeneity								
Simpson	.71	.72	.25	.82	.69	.65	.61	.64
Shannon (H')	1.50	1.68	.63	1.99	1.43	1.33	1.33	1.45
Evenness								
Pielou (J')	.54	.56	.26	.67	.60	.54	.58	.63

Table 3. Communities compared by the Quotient of Similarity (Sorensen coeffiecient).

	TOTW	*TOTS*	*MFS1*	*MFS2*	*RTW1*	*RTW3*	*RTW5*
TOTS	.556						
MFS1	.444	.710					
MFS2	.556	1.000	.710				
RTW1	.815	.516	.545	.516			
RTW3	.857	.500	.435	.500	.783		
RTW5	.769	.600	.476	.600	.762	.727	
RTW8	.769	.467	.476	.467	.762	.727	.800

See Table 1 for code.

compared to the pooled data. The savanna transects were 71% similar to each other, but only 56% similar to the woodland.

A relative abundance curve of ants from Middlefork Savanna showed (Figure 1) a log normal pattern of species abundance. This is indicative of a natural habitat having a large, mature, and varied community (Magurran, 1988).

Additional research is needed to clearly identify the distinctive ant fauna characteristic of prairies, savannas, woodlands, and true forests. Only then can the faunas be accurately compared and the effects of human-caused degradation be assessed.

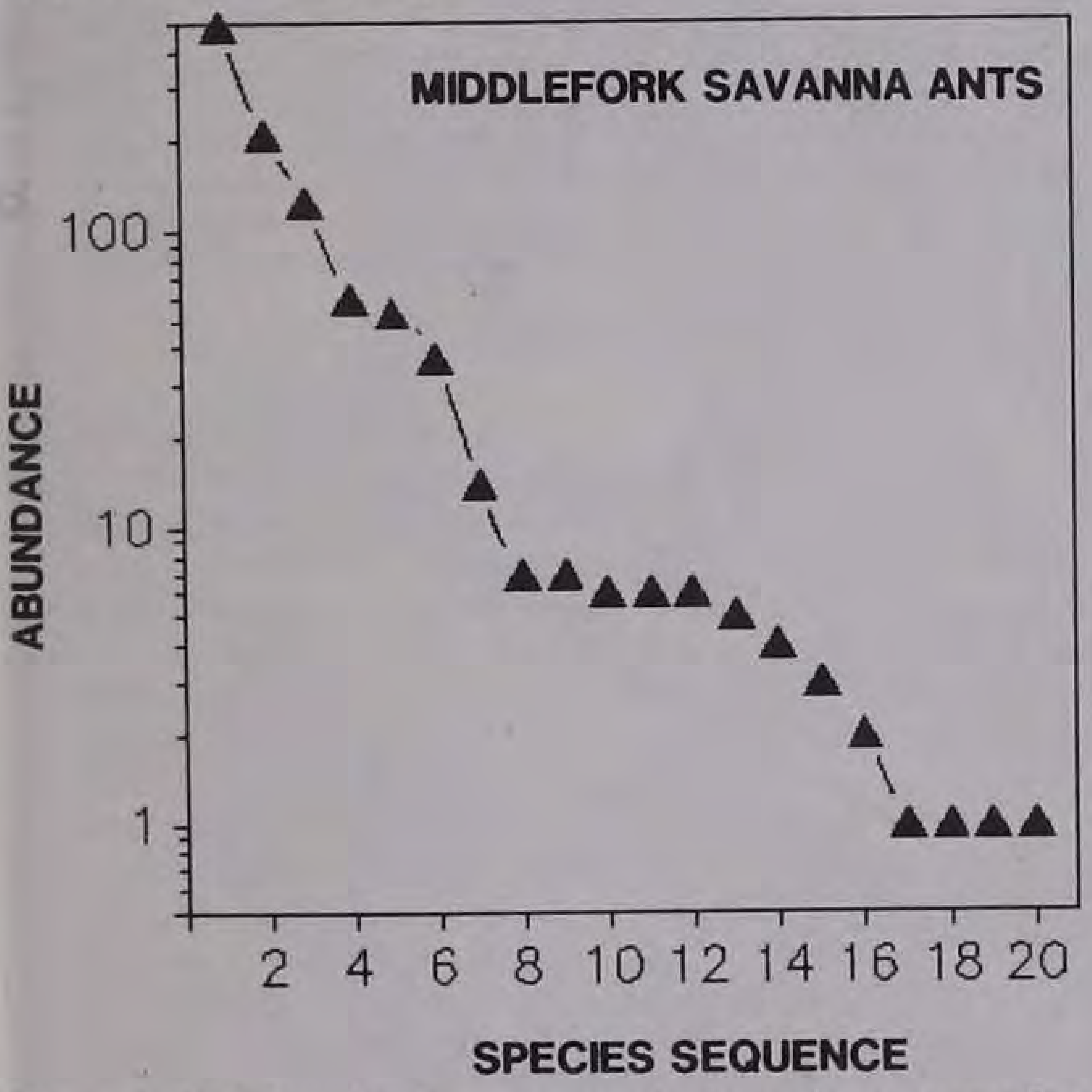

Figure 1. Relative abundance, or species importance, curve for ants collected from Middlefork Savanna.

ACKNOWLEDGEMENTS

Steve Apfelbaum of Applied Ecological Services made this study possible. Collecting and a portion of the identification were supported by a grant from the Illinois Nongame Checkoff Fund Program to Applied Ecological Services. Dr. Mark DuBois provided valuable advice to help us identify the ants and to confirm the identification of some species. To the above, we extend our deep appreciation.

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ECOLOGICAL ASPECTS OF THE KNIFE RIVER INDIAN VILLAGES NATIONAL HISTORIC SITE, WEST-CENTRAL NORTH DAKOTA

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Abstract. This 520-hectare site was a focal point for 18th and early 19th century Native American settlement along the upper Missouri River. Remnants of native ecosystems still remain, and an ecological analysis is integral to historic interpretations and contemporary management. Ground surveys throughout the growing season, quadrat sampling, aerial photo-interpretation, and review of historic records were used to characterize the flora and vegetation. The flora consists of at least 257 taxa, of which 49% are primarily prairie inhabitants, 16% usually appear in forests, 22% are ruderal species, and 13% occur in moist habitats. The percentages of the area in various cover categories include prairie (18.2), grass/shrub mixture (16.6), forest (25.3), river surface (5.2), sandbars (3.8), revegetated former cropland (25.8), cropland (4.4), roads and trails (0.6). The uncultivated uplands consist of mixed-grass prairie dominated by needle-and-thread, *Stipa comata* Trin. & Rupr.; blue grama, *Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths; threadleaf sedge, *Carex filifolia* Nutt.; junegrass, *Koeleria pyramidata* (Lam.) Beauv.; and western wheatgrass, *Agropyron smithii* Rydb. Mesic vegetation occurs at lower elevations and grades into shrublands and forests closer to the rivers. The forests are of two types: green ash (*Fraxinus pennsylvanica* Marsh.)-boxelder (*Acer negundo* L.)-American elm (*Ulmus americana* L.) and cottonwood (*Populus deltoides* Marsh.). Both types have been affected by earlier human disturbance.

INTRODUCTION

Historical Background

The Knife River Indian Villages National Historic Site (KNRI), located at the confluence of the Knife and the Missouri rivers in west-central North Dakota, was established in 1974 to preserve historic and archaeologic remnants related to Plains Indian culture (Hellickson-Key 1984). Three major Indian villages were located there during the 18th and early 19th centuries. These and other nearby sites indicate this was a settlement center for the Mandans and Hidatsas—thriving cultures supported by agriculture, hunting/gathering, and trading (Lovick and Ahler 1982).

For approximately four decades, beginning in the 1790s, this site was also a significant contact point with Euro-Americans. It became a trading center and an area visited by various explorers and travelers. The Lewis and Clark Expedition, on its way up the Missouri River, overwintered several miles away during the winter of 1804-05. Later came naturalists and artists, such as Bradbury, Brackenridge, Nuttall, Catlin, Maximilian (Prince of Wied), Bodmer, and Audubon (Clambey 1985).

Smallpox epidemics, cultural change triggered by intercultural contact, and Dakota Indian raids decimated the tribes in the 1830s. Survivors abandoned the villages by 1845 and moved farther upstream. Euro-American settlement around the site began 30-40 years later. Cropping, grazing, and some timber harvesting on the floodplain continued until acquisition of the 520-ha site in 1976-1980.

Climate

This region, with its mid-continental location, experiences semi-arid conditions with large seasonal temperature variations (Jensen 1972, Mack 1981, Wilhelm 1978). Average annual precipitation is 41.1 cm, but over an 88-year period, it ranged from 14.5 to 68.6 cm/yr. Mack (1981) found that drought conditions were often exacerbated by a coincidence of high temperatures with low precipitation. The majority of moisture is received during the growing season, which is approximately 120 days. July, the warmest month, averages 21.2 C; January, the coldest month, averages -13.3 C. During a year, temperatures can differ by 65 C or more.

Geologic and Soil Conditions

Reiten (1983), who investigated a 300 km area around KNRI, concluded that land surfaces had been shaped by glacial, alluvial, and aeolian action. He identified five distinct surfaces or terraces within the river valleys at KNRI. In decreasing order of elevation and age, these are the Hensler terrace (Pleistocene Epoch, approximately 22,000 years), Stanton terrace (Late-Pleistocene Epoch, 13,000 years), A terrace, B1 terrace, and B2 terrace. The last three are Holocene alluvial deposits aged at approximately 4500 years, less than 2500 years, and 340 years or less, respectively.

The Hensler terrace consists of 10-16 m of fluvial sand and gravel, capped by variable amounts of aeolian sand and silt (Reiten 1983). Reiten described the Stanton terrace as composed of over 2 m of poorly sorted sand and gravel overlain by up to 5 m of aeolian silt or clay. Deeper portions of the A terrace consist of silty sand and clay, above which is a meter of clayey silt, capped by as much as a meter of silt. Silty clay materials predominate in the B1 terrace. The B2 terrace, which is the current floodplain, includes several meters of silty sand with an upper layer of silty clay and interspersed areas of sand.

Objectives of This Study

This work was carried out to provide an ecological inventory to facilitate natural history interpretation and site management. The principal objectives were to complete a floristic inventory and establish a reference plant collection, to map and analyze vegetation patterns, and to quantitatively describe the native grasslands and forests.

METHODS

Site Inventory

Ground reconnaissance and the floristic inventory were done during May-September 1984. Voucher specimens for most taxa were collected and prepared for deposition at the KNRI Headquarters. Scientific nomenclature used in this paper is based on the *Flora of the Great Plains* (Great Plains Flora Association 1986). Vegetation mapping was completed by combining the four months of field observations with aerial photographs taken in 1983 by the U.S. Department of Agriculture, Agricultural Stabilization and Conservation Service.

Quantitative Sampling

To characterize the remaining native grasslands, 28, 100-m^2 plots were positioned subjectively to represent the varied topographic and edaphic conditions. Twenty-five, 1/4-m^2 quadrats were then positioned randomly in each plot, and visual estimates of aerial plant cover were made for each species rooted in each quadrat. The results are expressed as relative cover values (percentages).

In the riparian forests, 83, 400-m^2 circular quadrats were positioned randomly along transects. All woody stems with a diameter-at-breast-height (DBH) of 2.5 cm or greater were recorded by species, and trunk cross-sectional areas (basal areas) were measured. Five, 1-m^2 circular quadrats were nested within each of the large quadrats. Here, tree seedlings and saplings were counted, and visual cover estimates were made for shrubs and herbaceous plants. To estimate tree ages, small sample cores were extracted from 30 subjectively selected trees and annual growth rings were counted.

RESULTS AND DISCUSSION

Floristic Inventory

A total of 257 vascular plant taxa were identified during the study. These represented 174 genera and 57 families. The families with the most representatives were the Asteraceae (50 species), Poaceae (35), Fabaceae (21), Rosaceae (15), and Brassicaceae (13).

All but four of the species are angiosperms, the exceptions being three species of horsetails and one gymnosperm shrub. Nearly 90% of the species are herbaceous, including 48 graminoids (grasses, sedges, and rushes), 2 succulents, and 180 forbs (herbaceous plants which are neither grasslike nor succulent). The remaining 27 woody species consist of 6 trees, 19 shrubs, and 2 vines.

Four habitat categories—prairie, forest, moist areas, and disturbed areas—were used to indicate where species are most likely to occur, based on field observations and literature sources. Almost half of the species (49%) are primarily prairie inhabitants. More than a fifth (ca. 22%) usually appear in areas disturbed by various human activities, such as cultivation, grazing, and construction. Forty-one species (ca. 16%) are largely forest species. Moist areas included sandbars, riverbanks, and depressions within prairies and forests. Thirty-four species (ca. 13%) are typical of such habitats.

Geographic origins and ranges of the species were determined by referring to several taxonomic sources (Gleason and Cronquist 1963, Great Plains Flora Association 1986, Stevens 1963, Stubbendieck et al. 1982, Van Bruggen 1976). Not surprisingly, because of the anthropogenic effects noted earlier, introduced species constitute a sizable part of the flora (15.2%). The native species represent a combination of plants derived from eastern and western parts of North America. This is typical of the North Dakota flora (Stevens 1920, Barker et al. 1976). The state has a derived flora and lacks endemic species. Species considered uncommon at the site are at the margins of their geographic ranges and can be found elsewhere in abundance. Reference to the latest state list of endangered and threatened vascular plants (Endangered and Threatened Vascular Plant Subcommittee 1985) revealed no KNRI plants in either category.

Vegetation Patterns

Using the 1983 aerial photographs, ground observations, and a point-sampling grid, the area of each of several surface cover-types was estimated. Prairie covered 18.2% of the site. Prairie and shrubland mixtures added another 16.6%. Such areas, which included prairie constituents together with introduced pasture species and native shrubs, probably have resulted from a combination of species introductions, intensive grazing, and fire exclusion. Former cropland represented 25.8% of the site. Prior to human habitation, most of this would have been prairie. Before completing sale of the cropland to the National Park Service the landowners were required to reseed grass cover. This was done with varied success, and individuals chose any of several native or introduced perennial grasses. Riparian forests covered 25.3% of the site. Their extent was perhaps not too different from pre-settlement time, but, as noted subsequently, there have been qualitative changes. The Knife River water surface extended over 5.2% of the area, and sandbars along the Knife and Missouri rivers represented 3.8% of the site. Cropland (two small hayfields) accounted for 4.4%. Roads and trails made up the remainder, about 0.6%.

Native Grassland Composition

KNRI occurs within a region of primarily mixed-grass prairie (Whitman and Wali 1974). Before modern settlement, most of the site was undoubtedly grassland. Despite the modest size of the site (520 ha) and past human impact, the remaining grasslands exhibit heterogeneity related to topography, soil conditions, and anthropogenic factors. Because topography exerts a major influence on vegetation, the data were summarized relative to the five units (terraces).

Thirteen sets of 25 quadrats were sampled on the upland and slope portions of the Hensler terrace. It is the highest land surface, and it supports the majority of the remaining grasslands. There, the predominant graminoids and their relative cover values were needle-and-thread (17.8%), blue grama (16.9%), threadleaved sedge (12.7%), junegrass (4.0%), and western wheatgrass (3.0%). Leading the forb category were green sage (*Artemisia dracunculus* L., 8.8%), white aster (*Aster ericoides* L., 4.7%), fringed sage (*Artemisia frigida* Willd., 4.4%), skeletonweed (*Lygodesmia juncea* (Pursh) Hook., 3.4%), and dotted gayfeather (*Liatris punctata* Hook., 3.3%). The average number of vascular plant species per set of quadrats was 23.0.

Small drainageways and depressions also exist on the Hensler terrace. Four sets of quadrats were sampled in such habitats. The average number of species per set was 29.0. Not only did the more mesic conditions foster greater diversity, but there was a shift of dominants. Kentucky bluegrass (*Poa pratensis* L., 20.3%) thrived here. Needle-and-thread (7.4%) and blue grama (6.4%) were less abundant and were joined by big bluestem (*Andropogon gerardii* Vitman, 4.2%), a common constituent of tallgrass prairies, and green needlegrass (*Stipa viridula* Trin., 4.1%). The leading non-graminoid was a shrub, western snowberry (*Symphoricarpos occidentalis* Hook., 10.5%), followed by white aster (5.6%), pasture sage (*Artemisia ludoviciana* Nutt., 4.3%), blue lettuce (*Lactuca oblongifolia* Nutt., 3.1%), green sage (2.7%), and purple coneflower (*Echinacea angustifolia* DC, 2.7%)

In one part of the site, a portion of the Stanton terrace is at the base of the Hensler terrace. Here, there is possibly supplemental moisture from runoff and infiltration, while elsewhere the Stanton terrace is the highest surface because erosion had erased the Hensler terrace. In the former instance, two sets of quadrats were placed in areas of fine-textured soils, and two other sets were placed on areas of coarser-textured soils formed by alluvial fans. Both would have been near the margins of the largest Indian village site and, as such, must have experienced prolonged human impact.

On the fine-textured soils, diversity was low, with only 14.5 species per set of quadrats. Western wheatgrass (27.9%), Kentucky bluegrass (24.6%), and green needlegrass (18.3%) were prevalent. Present in small quantities were blue grama (3.9%) and needle-and-thread (0.6%). Heading the list of forbs were white aster (8.3%), pasture sage (5.1%), yarrow (*Achillea millefolium* L., 4.2%), and globe mallow (*Sphaeralcea coccinea* (Pursh) Rydb., 3.0%). There was one shrub, prairie wild rose (*Rosa arkansana* Porter, 1.1%).

On the coarse-textured soils, diversity was notably higher, 32.0 species per set of quadrats. Species common here included big bluestem (29.6%), needle-and-thread (10.2%), little bluestem (*Andropogon scoparius* Michx., 4.9%), blue grama (4.7%), and junegrass (4.3%). Non-graminoids with the highest relative cover values were pasture sage (5.8%), silverleaf scurfpea (*Psoralea argophylla* Pursh, 5.2%), white aster (4.9%), blue lettuce (2.6%), and prairie wild rose (1.6%).

Four sets of quadrats were placed on portions of the Stanton terrace where it represented the uppermost land surface. Diversity was similar to that on the Hensler terrace, 24.6 species per set of quadrats, as compared to 23.0. Here, the grassland was dominated by blue grama (14.8%), needle-and-thread (13.9%), western wheatgrass (11.7%), Kentucky bluegrass (11.0%), and plains muhly (*Muhlenbergia cuspidata* (Torr.) Rydb., 4.5%). Forbs with the highest relative cover values included fringed sage (5.9%), silverleaf scurfpea (4.8%), scarlet gaura (*Gaura coccinea* Pursh, 3.7%), white aster (3.3%), and blue lettuce (2.5%).

There was a small area of the A terrace with prairie vegetation. It occurred near the margin of a second Indian village site, downslope from an adjacent portion of the Stanton terrace. Nineteen species were found in one set of quadrats. Kentucky bluegrass (33.3%), western wheatgrass (25.5%), green needlegrass (12.8%), blue grama (6.4%), and needle-and-thread (1.5%) composed most of the graminoid cover. Globe mallow (3.4%), western snowberry (3.4%), green sage (2.9%), pasture sage (2.9%), and fringed sage (1.5%) contributed most to a limited non-graminoid component.

The B1 and B2 terraces, being the lowest and closest to the rivers, have been viewed as exclusively forest habitat, yet that is not the case. A localized grassland area on the B1 terrace was covered largely by big bluestem (62.4%), plus some Kentucky bluegrass (4.6%), sideoats grama (*Bouteloua curtipendula* (Michx.) Torr., 3.2%), green needlegrass (1.4%), and smooth brome (*Bromus inermis* Leyss., 0.5%). The leading forbs were silverleaf scurfpea (10.3%), Flodman's thistle (*Cirsium flodmanii* (Rydb.) Arthur 3.8%), pasture sage (2.7%), fringed sage (2.5%), and Canada anemone (*Anemone canadensis* L., 2.2%). Twenty-two species were found in the one set of quadrats sampled.

The B2 terrace, the current floodplain, though commonly wooded, also includes sandy soils harboring small grassland or shrubland areas. One such area was sampled, and 19 plant species were found in that quadrat set. As on the the dry uplands, blue grama (13.5%), needle-and-thread (7.4%), threadleaved sedge (5.0%), and junegrass (5.0%) were leading species. Prairie sandreed (*Calamovilfa longifolia* (Hook.) Scribn., 7.1%), only a scattered constituent on the upland, was more frequent here. Likewise, fringed sage (16.8%) and dotted gayfeather (4.7%) appeared here. Prairie wild rose (7.9%) and golden aster (*Chrysopsis villosa* (Pursh) Nutt., 12.4%) were more abundant in this area, as were forbs and shrubs in general. Lemon scurfpea (*Psoralea lanceolata* Pursh, 5.9%) was unique to these low dune areas.

Across the complex environmental gradient represented by the series of land surfaces, one can see species in varied combinations. Each combination might be seen as a distinct community or as a shifting set of species, few of which are unique to any single area. The overall character of the grasslands is a mixed-grass prairie with local variations, including occasional tallgrass prairie outliers.

Native Forest Composition

Forests of the site fell into two categories: those dominated by cottonwood and more extensive areas where there were few or no cottonwoods. The latter forests, which were dominated by green ash, with some boxelder and American elm, had experienced different amounts of impact by earlier timber harvest and grazing.

Cottonwood and peachleaf willow (*Salix amygdaloides* Anderss.), which require open, moist conditions for establishment, appeared on young geologic surfaces formed by river action—pointbars, islands, shoreline deposits, and abandoned channels. Such features appeared near the confluence of the Knife and Missouri rivers, where five such wooded strips occurred.

The cottonwood-willow forests were relatively massive, containing large diameter trees and high canopies (20-25 m), yet the trees were only 37-75 years old. This indicates the rapid growth rate of cottonwood and the suitable conditions available near the rivers. Average tree density was 335.4 trees/ha, with 73.9% of those being cottonwood; 24.2%, peachleaf willow; and 1.9%, Russian olive (*Elaeagnus angustifolia* L.), an introduced species able to occasionally invade openings within these forests. Tree basal area, an expression of dominance as cross-sectional trunk area per unit land area, averaged 39.9 m^2/ha. The predominance of cottonwood was even more evident here, as it contributed 85.8% of total basal area. Willow represented most of the remainder, with small Russian olive trees contributing about 0.1% of the total.

Beneath the somewhat open canopy, there was sufficient light for extensive understory development; however, that was limited locally by the droughty nature of the sandy surface soils. Tree seedlings and saplings averaged 1.4/m^2. Cottonwood and willow exhibited no regeneration; the scattered seedlings/saplings were primarily green ash, with occasional elm and boxelder, a situation similar to that reported by Johnson et al. (1976) in an extensive study of Missouri River forests. Common shrubs included poison ivy (*Toxicodendron radicans* (L.) O. Ktze.), western snowberry, western wild rose (*Rosa woodsii* Lindl.), and Virginia creeper (*Parthenocissus vitacea* (Knerr) Hitchc). Smooth brome and Kentucky bluegrass were the most common herbaceous plants. Other moderately abundant herbaceous plants included Virginia wild rye (*Elymus virginicus* L.), western wheatgrass, hog peanut (*Amphicarpaea bracteata* (L.) Fern.), American vetch (*Vicia americana* Muhl. ex Willd.), common milkweed (*Asclepias syriaca* L.), and Canada thistle (*Cirsium arvense* (L.) Scop.).

If a land surface within these river valleys is stable for some time, forest succession continues, and the fast-growing, shortlived cottonwood and willow are supplanted by green ash, boxelder, and American elm, which are able to invade and reproduce (Johnson et al. 1976). While all such ash-boxelder-elm areas within KNRI have experienced human impact, a few have been less disturbed. Looking first at these, average tree density was 888.7 trees/ha. Green ash and boxelder had 51.8% and 45.1%, respectively, with 2% attributable to American elm, 0.6% to cottonwood, and 0.5% to peachleaf willow. Tree basal area averaged 34.7 m^2/ha, consisting of green ash (72.4%), boxelder (14.4%), cottonwood (8.5%), American elm (3.5%), and willow (1.1%). The few cottonwoods were large individuals. Although Dutch elm disease had struck the area, the abundance of elm was unusually low. Young boxelders were abundant and contributed to the relatively high density, but many of these will succumb to competition with larger trees. The forest character was especially shaped by vigorous green ash, which formed a fairly dense canopy reaching to about 20 m. Despite their large size, the largest ash trees cored ranged in age from only 66 to 87 years.

In the less disturbed areas, tree regeneration was evident (5.3 seedlings and saplings/m^2) and consisted largely of green ash and boxelder, plus occasional elm. Two of the areas had few shrubs and vines; a third area had poison ivy as a frequent understory component. The sparse herbaceous understory included Virginia wild rye, Kentucky bluegrass, bedstraw (*Galium triflorum* Michx.), dame's rocket (*Hesperis matronalis* L.), pellitory (*Parietaria pensylvanica* Muhl.), and stinging nettle (*Urtica dioica* L.)

The preceding forests, although showing evidence of some earlier grazing use, were in better condition than most of the forest areas, which had apparently experienced more cutting and grazing pressure. In these more disturbed areas, still marked by fenceline remnants, the tree canopy was only 10-12 m high. Tree density averaged 423.5 trees/ha and basal area, only 20.9 m^2/ha. Of the trees, 58.5% were ash, 29.3% boxelder, 8.9% elm, 3.2% cottonwood, and 0.1% peachleaf willow. Compared to the two types of less disturbed forests, it can be seen that these ash-boxelder forests are lower stature with smaller individuals and, hence, have a more open canopy. Tree ages were similar to those of the less disturbed ash-boxelder areas; however, trees were smaller, perhaps because of less favorable soil conditions and a history of much more intense pasture use. Nearly half of the trees had noticeable canopy dieback or breakage, and signs of a heart-rot fungus (*Fomes fraxinophili*) were seen with many trees.

Meanwhile, there was little tree regeneration. Seedling/sapling density was only 1.1/m^2, and many of these were current-year seedlings that did not survive the growing season. The reason for the hiatus could be seen in the understory. Four of the five areas had an essentially continuous understory of smooth brome that was waist-high by mid-growing season. A fifth area had a dense understory of tall poison ivy. In all cases, such growth limited tree regeneration and overall understory diversity.

Implications

This analysis of the flora and vegetation revealed that many of the natural constituents remained. These can contribute to both interpretive and management efforts. Still, much needs to be done for site restoration. Prescribed burning would improve the condition of mesic grassland and shrubland areas while reducing the hazards of wildfires. Some efforts to reseed former cropland were ineffective, and renewed efforts at grassland restoration are in order. Some forest areas are in reasonably good condition; others will take many years to recover. These ecological aspects, together with the archaeological evidence, can be interwoven to tell visitors a story of human-environment relations on one part of the northern Great Plains during the past 200 years.

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SPECIES COMPOSITION OF OLD SETTLER SAVANNA AND SAND PRAIRIE CEMETERIES IN NORTHERN ILLINOIS AND NORTHWESTERN INDIANA

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Abstract. Over the course of a decade, studies were conducted throughout northern Illinois and northeastern Indiana to locate old settler cemeteries containing prairie vegetation and to determine their species composition. These studies were part of an effort to determine the presettlement vegetation of these areas. Forty-five cemeteries identified as having 30 or more prairie species were considered of sufficient quality to warrant further study. This paper reports on 16 cemeteries not reported in an earlier paper. Of these, eight were silt-loam savanna prairies, six were sand savanna prairies, one was a silt-loam-sand-gravel savanna prairie, and one was a sand prairie. A total of 238 prairie and savanna species, belonging to 55 families, were found in them. The *Compositae* had the most representatives with 61 species (26%), followed by the *Gramineae* with 24 (10%), the *Leguminosae* with 20 (8%), and the *Cyperaceae* with 11 (5%). With the exception of the sand prairie, the soils present in these cemeteries had relatively shallow A horizons, and all showed no evidence of ever having been plowed. The difference in soil type (silt-loam, sand, gravel) influenced species composition and relative abundance. Most of the savanna cemeteries were associated with various oaks (*Quercus*) and hickories (*Carya*).

INTRODUCTION

In an effort to gain insight into the species composition of the presettlement Illinois-Indiana prairies, extensive searches were conducted during the 1970s throughout northern Illinois and northwestern Indiana to find old settler prairie cemeteries and to study their species composition. During the course of these studies, it became apparent that in 15 cemeteries, prairie species were found in association with native woody vegetation (trees or shrubs) characteristic of savannas (Curtis 1959; Bray 1960). Because these savanna cemeteries proved to be sufficiently different from the 29 silt-loam prairie cemeteries reported earlier (Betz and Lamp 1989), it was decided to report on these savanna cemeteries separately.

One other prairie cemetery was also sufficiently different to warrant separation from the silt-loam prairie cemeteries. This was the sand prairie cemetery included in this study (Cemetery 10, see Table 1).

The vegetation of these 16 cemeteries is compared to that of the 29 silt-loam prairie cemeteries. In addition, the relationship of these savanna cemeteries to presettlement groves and barrens and the savannas described by Curtis (1959) and Bray (1960) are also discussed.

Even though many ecological texts mention that remnant prairies are to be found in old settler cemeteries, they are actually described in relatively few papers. Lantz (1969) and Morrissey (1956) reported on the species composition of two different cemetery prairies in Iowa, and cemetery prairies were used in studies by Fay (1953) in Iowa and by Penalosa (1963) in California. Wright and Wright (1948) used old settler cemeteries as a source of data to study the ecological relationships existing between the Palouse and mixed-grass prairies in south-central Montana.

Although the Illinois-Indiana tallgrass prairie and savanna are known through historical accounts, their species compositions are not well documented. Most of the early reports (Short 1845) were of a general nature, with such vague names as goldenrods, asters, etc. Some information about the prairies' composition can be gleaned from the annotated plant lists of Mead (1846) and Brendel (1887). In this century, species composition studies include 1) the Illinois sand prairies (Gleason 1910), 2) the sand prairie of the beach area in northeastern Illinois (Gates 1912), 3) the hill prairies along the Mississippi (Evers 1955), and 4) the hill prairies along the Rock River in northern Illinois (Fell and Fell 1956). In addition, both Vestal (1914) and Sampson (1921) reported on the heavier silt-loam prairies of northern Illinois, and Betz and Cole (1969) recorded the vegetational changes that occurred on a black-soil prairie originally studied by Paintin (1928).

There are few studies on Illinois savannas. Packard (1988) reported on the restoration of tallgrass savanna and listed some characteristic savanna species. Both Kilbourn (1959) and Moran (1978) used land survey records to determine the presettlement distribution of savannas and their woody composition in two counties of northern Illinois. The species composition of oak savannas and barrens in southern Wisconsin has been studied by Curtis (1959) and Bray (1960).

The focus of this study was not the trees and other woody vegetation associated with the savanna cemeteries but rather the herbaceous vegetation. This paper lists only trees present. We feel, however, that a fuller understanding of the original presettlement woody vegetation for these savanna cemeteries may be gained from original land survey records. Such a study is planned and will be reported in a later paper.

METHODS

Using general highway maps, prepared by the Illinois Department of Public Works and Buildings, that cover individual counties and show the locations of cemeteries, visits were made to all cemeteries within selected areas. However, it soon became evident that many of the cemeteries had originally been wooded areas and did not have the potential to contain surviving prairie vegetation. Based on this consideration, it was decided to restrict exploratory visits to cemeteries on original prairie or prairie-forest transition areas as determined by the soil types found for the cemeteries. Accordingly, soil reports and maps prepared by the Agricultural Experiment Station of the University of Illinois in cooperation with the Soil Conservation Service of the U.S. Department of Agriculture were used for this purpose. Only cemeteries having soil types characteristic of prairie or prairie-forest transition were selected for examination, and thus, the number of cemeteries designated for study was reduced substantially.

In each cemetery, certain prairie indicator species were sought, especially the warm-season grasses, such as big bluestem (*Andropogon gerardii* Vitman) and Indian grass (*Sorghastrum nutans* (L.) Nash). These grasses often persisted around tombstones and in fence rows, even in those cemeteries which had been heavily mowed. In many cases, the entire cemetery was still prairie. In others, prairie vegetation was to be found only in relatively undisturbed sections, such as areas along the perimeter. Cemeteries that were being regularly mowed were checked for depauperate prairie plants, such as lead plant (*Amorpha canescens* Pursh), wild bergamot (*Monarda fistulosa* L.), and yellow coneflower (*Ratibida pinnata* (Vent) Barnh.). These were sometimes found surviving mowing within the Kentucky bluegrass (*Poa pratensis* L.) turf. For most cemeteries, efforts were made to urge the cemetery boards to cease mowing, so that enhanced growth would better permit the determination of the species composition of the remnant prairies. Agreement was reached in many instances.

Vascular plants present were recorded at the time the cemeteries were initially visited. If the cemetery had at least 30 prairie species, a more extensive study was conducted. This necessitated revisiting the cemetery prairie at various times throughout the growing season for two or more years. Several prairie cemeteries were visited more than a dozen times in order to catalog all the species. Nomenclature follows that of Fernald (1950) and conforms with Swink and Wilhelm (1979). In addition to recording the species present, soil samples were taken to determine the depth of the A horizon and to note other soil characteristics, such as the soil type.

Of the 825 cemeteries surveyed in 42 counties of northern Illinois and in 20 counties of northwestern Indiana, 150 contained some prairie species. Of these, there were 16 sand prairie and savanna cemeteries that had more than 30 prairie species and were deemed worthy of further study.

Each of these 16 cemeteries is designated in the text and tables by number (1-16). Each cemetery was also identified by the county in which it occurred, followed by a number indicating the order in which the cemetery was visited in that county (Table 1). If a name for the cemetery was known, it was placed in parenthesis following the number. For example, Cemetery 5 is Livingston 3 (Campbell). That is, the Campbell Cemetery was the third cemetery prairie observed in Livingston County in northeastern Illinois.

Table 1. Total number of species and size in Illinois-Indiana sand prairie and savanna cemeteries.

Cemetery name and number	*No. of species*	*Hectares*
Silt-loam savannas		
Cem 1-Bureau 2 (North Princeton)	33	0.4
Cem 2-Bureau 3 (Tiskilwa)	41	0.4
Cem 3-Carroll 1 (Brookville)[1]	38	0.4
Cem 4-Knox 1 (Copely)	75	0.8
Cem 5-Livingston 3 (Campbell)	50	0.4
Cem 6-Will 3 (Monee)	33	0.2
Cem 7-Will 4 (Scheer)	52	0.4
Cem 8-Warren-Ind 1 (Brisco)[2]	30	0.4
Silt-loam/sand/gravel/savanna		
Cem 9-Tazewell 1 (Bequaith)	45	0.4
Sand prairie		
Cem 10-Whiteside 3 (Springhill)	53	0.8
Sand savannas		
Cem 11-Grundy 1 (Short)[1]	45	0.4
Cem 12-Henderson 1 (no known name)	47	0.4
Cem 13-Kankakee 1 (Essex)	56	0.4
Cem 14-Ogle 2 (no known name)	45	0.4
Cem 15-LaPorte-Ind 1 (Morgan)	28	0.8
Cem 16-Will 2 (Braidwood-Oakwood)	105	0.8

[1] Illinois Nature Preserve.
[2] Indiana Nature Preserve.

RESULTS

Of the 16 cemeteries reported on in this paper, one was a sand prairie, eight were silt-loam savannas, six were sand savannas and one was a silt-loam-sand-gravel complex savanna. These cemeteries varied in size from 0.4 to 0.8 ha (Table 1).

The 238 prairie or savanna species found in these cemeteries represent 55 families (Table 2). The *Compositae* had the most representatives with 61 species (26%), followed by the *Gramineae* with 24 (10%), the *Leguminosae* with 20 (8%), and the *Cyperaceae* with 11 (5%). There were 133 species of plants observed in the eight silt-loam savanna prairies (Cemeteries 1-8) and 157 species in the six sand savanna prairies (Cemeteries 11-16). Some species, such as the dominant prairie grasses, big bluestem (*Andropogon gerardii* Vitman), little bluestem (*A. scoparius* Michx.), and Indian grass (*Sorghastrum nutans* (L.) Nash), were found in most of the cemeteries regardless of the soil type. Others were more restricted. For example, the smooth blue aster (*Aster laevis* L.), which is characteristicly found on silt-loam soils, was only in one silt-loam savanna cemetery. The slender bush clover (*Lespedeza virginica* (L.) Britt.) was found only in one sand savanna prairie cemetery.

The number of species found in the silt-loam savannas varied from 30 in Cemetery 8 (Brisco Cemetery, Warren County, Indiana) to 75 in Cemetery 4 (Copely Cemetery, Knox County, Illinois) (Table 1). The number of species found in the sand savannas varied from 28 in Cemetery 15 (the Morgan Cemetery, LaPorte County, Indiana) to 105 in Cemetery 16 (Braidwood-Oakwood Cemetery, Will County, Illinois) (Table 1). In addition to these 238 prairie or savanna species, there were 22 species of woody plants, including black oak (*Quercus velutina* L.), bur oak (*Q. macrocarpa* Michx.), shagbark hickory (*Carya ovata* (Mill.) E.Koch), and hazelnut (*Corylus americana* Walt.).

There were 54 species of weedy native or non-native herbaceous plants. These included Kentucky bluegrass (*Poa pratensis* L.), common peppergrass (*Lepedium virginicum* L.), old-field sorrel (*Rumex acetosella* L.), horseweed (*Erigeron canadensis* L.), and yarrow (*Achillea millefolium* L.). Further, there were 14 species of cultivated forbs, such as live forever (*Sedum purpureum* (L.) Link), orange day lily (*Hemerocallis fulva.* L.), cypress spurge (*Euphorbia cyparissias* L.), and star of Bethlehem (*Ornithogalum umbellatum* L.) The number and kind of these non-prairie, non-savanna species were dependent in part on the past management of the cemetery (mowing, grazing, trampling, or having decorative plants put on the graves). Non-prairie species were generally absent in cemetery prairies that had never been mowed, or had not been mowed for many years, and had been burned annually on a rather consistent basis.

DISCUSSION

Silt-loam Savannas (Cemeteries 1-8)

A comparison of these silt-loam savanna cemeteries with silt-loam prairie cemeteries (Betz & Lamp 1989) suggests four major differences. First, all of these savanna cemeteries had trees either scattered in the cemetery itself or along fences or adjacent to the cemetery. Bur oak (*Quercus macrocarpa* Michx.) was especially prominent, but other species of oak, such as white oak (*Q. alba* L), red oak (*Q. rubra* L.), and black oak (*Q. velutina* Lam.), were also present. Other woody plants occasionally present were shagbark hickory (*Carya ovata* (Mill.) Sarg., bitternut hickory (*C. cordiformis* (Wang) K.Koch), big shellbark hickory (*C. laciniosa* (Michx.) Loud), basswood (*Tilia americana* L.), red cedar (*Juniperus virginiana creber* Fern. & Grisc.), hazelnut (*Corylus americana* Walt.), wafer ash (*Ptelea trifoliata* L.), and smooth sumac (*Rhus glabra* L.).

Second, savanna cemeteries had a much shallower A horizon than prairie cemeteries. The depths of the A horizon in these savanna cemeteries ranged from 10 to 23 cm (Table 3) and were approximately half of the 12-45 cm observed for silt-loam prairie cemeteries. The savanna cemeteries on prairie/forest transition soils may have been the result of prairie vegetation invading formerly wooded tracts. The fact that these savanna cemeteries were usually adjacent to oak-hickory woodlands found along streams or

Table 2. Species Composition of Illinois-Indiana sand prairie and savanna cemeteries.

	Cemetery prairie number[1]																
Species[2]	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*Total[3]*
Agrimonia parviflora																X	1
Agrostis alba palustris																X	1
Agrostis hyemalis							X										1
Alisma subcordatum																X	1
Ambrosia psilostachya cor										X	X	X		X		X	5
Amorpha canescens				X	X	X	X		X	X	X	X	X	X		X	11
Amphicarpa bracteata				X									X			X	3
Andropogon gerardii	X	X	X	X	X		X	X	X	X	X	X	X		X	X	14
Andropogon scoparius		X	X	X	X		X	X	X	X	X	X	X	X	X	X	14
Androsace occidentalis											X	X		X			3
Anemone cylindrica				X			X			X		X	X			X	6
Antennaria neglecta	X		X	X	X		X			X		X	X			X	9
Antennaria plataginifolia			X	X	X		X	X		X		X	X		X	X	1
Apios americana			X														1
Apocynum androsaemifolium		X															1
Apocynum sibiricum	X		X														2
Arabis lyrata										X							1
Artemisia caudata											X		X	X			3
Asclepias amplexicaulis											X	X	X		X	X	5
Asclepias incarnata																X	1
Asclepias tuberosa	X					X									X		3
Asclepias verticillata	X			X	X		X		X	X	X	X	X	X		X	11
Asclepias viridiflora										X			X	X		X	4
Aster azureus				X	X		X								X	X	5
Aster ericoides		X		X		X	X		X							X	6
Aster laevis				X													1
Aster lateriflorus				X													1
Aster novae-angliae		X				X										X	3
Aster sagittifolius drum				X	X											X	3
Aster simplex																X	1
Aster umbellatus																X	1
Baptisia leucantha	X	X	X	X				X								X	6
Baptisia leucophaea						X				X							2
Bouteloua curtipendula													X				1
Bouteloua hirsuta												X					1
Cacalia atriplicifolia								X	X								2
Calamagrostis canadensis																X	1
Callirhoe triangulata									X	X	X						3
Caltha palustris																X	1
Camassia scilloides				X													1
Carex bicknellii	X	X	X	X	X				X								6
Carex brevior									X								1
Carex cephaloidea									X								1
Carex cephalophora												X					1
Carex cristatella				X													1
Carex gravida														X		X	2
Carex lanuginosum		X															1
Carex meadii										X							1
Carex pensylvanica	X				X		X										3
Carex stricta																X	1

Table 2. Continued

	Cemetery prairie number																
Species	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*Total*
Cassia fasciculata								X				X				X	3
Ceanothus americanus		X	X	X	X		X		X	X	X		X			X	10
Chenopodium leptophyllum											X		X	X		X	4
Chrysopsis camporum											X						1
Cicuta maculata																X	1
Cirsium discolor					X		X										2
Cirsium hillii				X	X												2
Cirsium muticum																X	1
Claytonia virginica					X												1
Comandra richardsiana	X	X		X	X	X		X	X				X	X			9
Convolvulus sepium		X															1
Coreopsis lanceolata											X		X	X			3
Coreopsis palmata					X	X				X		X		X			5
Coreopsis tripteris				X							X					X	3
Croton glandulosus sept									X							X	2
Cyperus filiculmis									X	X	X	X	X		X	X	7
Cyperus schweinitzii												X		X			2
Desmodium canadense	X	X		X	X											X	5
Desmodium glabellum					X												1
Desmodium illinoense		X	X	X			X			X	X	X	X			X	9
Desmodium sessilifolium								X							X		2
Dodecatheon meadia			X		X		X	X									4
Draba reptans														X			1
Dryopteris thelypteris																X	1
Echinacea pallida				X					X	X							3
Elymus canadensis		X							X								2
Equisetum hyemale										X	X		X		X	X	5
Eragrostis spectabilis									X	X	X	X	X		X	X	7
Erigeron strigosus	X	X	X	X	X		X		X	X	X	X	X	X		X	13
Eryngium yuccifolium	X			X			X										3
Eupatorium purpureum				X													1
Eupatorium perfoliatum																X	1
Eupatorium serotinum											X					X	2
Euphorbia corollata	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	15
Euphorbia dentata											X						1
Fragaria virginiana			X	X		X	X		X		X		X			X	8
Froelichia floridana												X					1
Froelichia gracilis													X				1
Galium obtusum				X													1
Galium triflorum				X													1
Gaura biennis											X					X	2
Gentiana andrewsii				X													1
Gentiana puberula				X			X										2
Gerardia grandiflora					X												1
Geranium maculatum		X						X								X	3
Geum canadense				X													1
Gnaphalium obtusifolium								X		X	X					X	4
Hedeoma hispida												X	X	X			3
Helianthemum bicknellii													X				1
Helianthemum canadense				X						X			X		X	X	5
Helianthus divaricatus								X	X								2
Helianthus grosseserratus		X	X	X		X										X	5

Table 2. Continued

	Cemetery prairie number																
Species	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*Total*
Helianthus laetiflorus	X		X	X		X										X	5
Helianthus mollis																X	1
Helianthus occidentalis				X	X		X			X	X	X	X	X	X	X	10
Helianthus strumosus		X															1
Heliopsis helianthoides			X	X					X								3
Heuchera richardsonii			X	X	X		X	X									5
Hieracium longipilum					X												1
Hypericum sphaerocarpum				X					X								2
Hypoxis hirsuta		X	X	X		X											4
Koeleria cristata							X					X		X		X	4
Krigia biflora			X	X													2
Krigia virginica												X					1
Kuhnia eupatoriodes										X				X			2
Lactuca canadensis			X						X				X	X			4
Lathyrus palustris																X	1
Lechea tenuifolia												X					1
Leptoloma cognatum									X		X		X		X	X	5
Lespedeza capitata	X	X	X	X	X		X	X	X	X	X	X	X	X		X	14
Lespedeza violacea								X									1
Lespedeza virginica													X				1
Liatris aspera						X				X				X	X		4
Liatris cylindracea					X												1
Liatris spicata																X	1
Lilium michiganense																X	1
Linaria canadensis												X		X			2
Lithospermum canescens				X		X	X	X		X							5
Lithospermum croceum										X	X	X	X	X			5
Lithospermum incisum											X						1
Lobelia spicata	X		X	X	X		X	X									6
Ludwigia alternifolia																X	1
Lycopus americanus				X													1
Lysimachia lanceolata							X										1
Lysimachia quadriflora						X											1
Lythrum alatum																X	1
Melica nitens									X								1
Monarda fistulosa	X	X	X	X	X	X	X	X	X		X					X	11
Monarda punctata										X							1
Myosotis verna					X												
Oenothera laciniata													X				1
Oenothera rhombiopetala												X	X	X		X	4
Onoclea sensibilis																X	1
Osmunda regalis																X	1
Opuntia humifusa											X	X	X		X	X	5
Oxalis violacea	X	X	X	X	X		X										6
Oxypolis rigidior																X	1
Panicum depauperatum														X			1
Panicum implicatum			X	X	X		X			X	X		X				7
Panicum leibergii				X		X											2
Panicum oligosanthes scr									X	X	X	X	X	X	X	X	8
Panicum villosisimum												X		X		X	3
Panicum virgatum									X					X		X	3
Parthenium integrifolium	X				X	X	X								X	X	6
Paspalum ciliatifolium													X				1

Table 2. Continued

	Cemetery prairie number																
Species	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*Total*
Pedicularis canadensis				X													1
Penstemon pallidus										X		X		X			3
Pentorum sedoides																X	1
Petalostemum candidum					X					X						X	3
Petalostemum purpureum				X	X		X						X				4
Phlox bifida										X	X		X				3
Phlox glaberrima inter																X	1
Phlox pilosa				X													1
Physalis heterophylla	X		X				X		X	X	X		X	X		X	9
Physalis virginiana							X			X		X	X		X		5
Plantago purshii											X			X			2
Polygala polygama										X				X			2
Polygala senega				X													1
Polygonatum canaliculatum						X			X		X						3
Polygonum coccineum																X	1
Polygonum tenue														X			1
Polytaenia nuttallii		X															1
Potentilla arguta					X		X			X			X	X			5
Potentilla simplex							X									X	2
Prenanthes aspera				X		X	X										3
Prenanthes racemosa																X	1
Prunella vulgaris lan.			X														1
Pteridium aquilinum la		X						X							X		3
Pycnanthemum tenuifolium				X													1
Pycnanthemum virginianum	X	X	X			X	X	X				X		X		X	9
Ranunculus fascicularis			X		X												2
Ratibida pinnata		X	X	X		X			X								5
Rosa carolina		X	X	X	X	X	X	X	X	X	X		X	X	X	X	14
Rudbeckia hirta	X	X		X	X		X	X	X	X			X	X	X	X	12
Ruellia humilis					X						X		X			X	4
Salix humilis		X	X	X				X							X	X	6
Saxifraga pensylvanica																X	1
Scirpus lineatus																X	1
Scrophularia lanceolata									X		X						2
Scrophylaria marilandica																X	1
Scutelaria parvula leon							X										1
Senecio plattensis	X									X	X	X		X		X	5
Silene stellata									X							X	2
Silphium integrifolium	X	X	X	X		X	X	X							X		8
Silphium laciniatum				X													1
Silphium terebinthinaceum	X	X			X	X	X										5
Sisyrinchium albidum	X		X	X	X	X	X			X						X	8
Smilacina racemosa								X									1
Smilacina stellata			X								X					X	3
Smilax lasioneura									X								1
Solidago altissima		X	X													X	3
Solidago gigantea		X		X										X			3
Solidago graminifolia						X										X	2
Solidago gymnospermoides																X	1
Solidago juncea	X			X			X	X								X	5
Solidago nemoralis					X			X		X	X	X			X	X	7
Solidago rigida		X	X	X	X	X	X								X		7
Solidago speciosa						X				X				X			3

Table 2. Continued

		Cemetery prairie number																
Species		*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*Total*
Sorghastrum nutans		X	X	X	X	X	X	X	X	X	X		X	X			X	13
Spartina pectinata																	X	1
Specularia perfoliata						X			X				X		X			4
Spiraea alba																	X	1
Spiranthes cernua								X										1
Sporobolus cryptandrus														X				1
Sporobolus heterolepis							X				X							2
Stachys tenuifolia																	X	1
Stipa spartea				X		X	X	X		X	X	X	X	X			X	10
Strophostyles leiosperma														X				1
Strophostyles helvola																	X	1
Taenidia integerrima					X											X		2
Talinum rugospermum													X					1
Tephrosia virginiana											X	X	X	X	X		X	6
Thalictrum dasycarpum																	X	1
Thalictrum dioicum						X												1
Thalictrum revolutum			X	X	X												X	4
Tradescantia ohiensis		X	X	X	X		X	X		X	X	X	X	X	X		X	13
Trillium recurvatum										X								1
Verbena hastata																	X	1
Verbena stricta		X	X							X	X	X	X	X	X		X	9
Vernonia fasciculata																	X	1
Veronicastrum virginicum			X		X					X							X	4
Viola papilionacea		X	X		X	X		X		X				X			X	8
Viola pedata						X		X									X	3
Viola pedatifida		X		X	X	X		X			X		X					7
Viola sagittata		X				X	X							X				4
Vulpia octoflora ten													X					1
Zizia aptera				X														1
Zizia aurea																X		1
Total	(odd #)	33		43		52		52		45		48		56		28		
	(even #)		41		75		34		30		53		47		46		110	
																		793

[1] The same number is used in both Tables 2 and 3 to designate a specific cemetery.

[2] Nomenclature follows Fernald (1950).

[3] The total number of cemeteries in which the species was found.

in isolated groves would tend to support this hypothesis. The persistence of prairie fires, whether natural or caused by Indians, may have opened the canopy of such woods by injuring or killing the trees. This in turn would have allowed the prairie to invade the woodlands. Observations made on the reestablished Fermilab Prairie, Batavia, Illinois, (Betz 1984) showed that older oaks could be killed and often toppled when prairie fires were allowed to burn into and through adjacent oak woodlands. This was especially true if the old trees had been previously injured by lightning, fungi, or carpenter ants. Under these conditions, the first prairie invader was usually Indian grass.

Third, although the range in number of species, both prairie and savanna, found in the savanna cemeteries (30-75) was approximately the same as that for prairie cemeteries (30-89), the mean numbers were quite different. The mean for the savanna cemeteries was 44; whereas, it was 59 for the true prairie cemeteries (Betz and Lamp 1989). In addition, only 109 prairie species were recorded for the savanna cemeteries. This was 60.6% of the 180 total prairie species recorded for prairie cemeteries.

Fourth, not only were these savanna cemeteries more limited in number of prairie species, but there were differences in species composition. White wild indigo (*Baptisia leucantha* T. & G.) was found in 6 of the 8 savannas (Table 2), while it was found in only 2 of the 29 prairie cemeteries (Betz and Lamp 1989). On the other hand, cream wild indigo (*B. leucophaea* Nutt.), which is usually associated with prairies, was found in 12 of the 29 prairie cemeteries (Betz and Lamp 1989), but in only one of the savanna cemeteries studied (Table 2). A few notable species of savannas and woodland edges associated with savanna cemeteries were spreading dogbane (*Apocynum androsaemifolium* L.), Drummond's aster (*Aster*

Table 3. Soils of savanna and sand prairie old settler cemeteries.

	Depth of A horizon (cm)	*Thickness of loess*
Silt-loam cemeteries		
Down-silt-loam		
Cem l-Bureau 2 (North Princeton)	18-20	over 152.4 cm
Cem 2-Bureau 3 (Tiskilwa)	13-15	"
Cem 3-Carroll 1 (Brookville)	15-18	"
Cem 4-Knox 1 (Copely)	10-18	"
Blount Sslt-loam		
Cem 5-Livingston 3 (Campbell)	10-18	45.5-91 cm
Beecher silt-loam		
Cem 6-Will 3 (Monee)	10-18	45.5-91 cm
Cem 7-Will 4 (Scheer)	18-23	"
Soil not determined		
Cem 8-Warren-Ind 1 (Brisco)	—	——
Intermediate silt-loam/sand cemeteries		
Burkhart-saude sand-gravel complex		
Cem 9-Tazewell 1 (Bequaith)	10-13	under 45.7 cm
Sand cemeteries		
Sparta sand (Prairie)		
Cem l0-Whiteside 3 (Springhill)	23-25	——
Plainfield sand (Savanna)		
Cem 11-Grundy 1 (Short)	5-10	——
Cem 12-Henderson 1 (no known name)	"	——
Cem 13-Kankakee 1 (Essex)	"	——
Cem 14-Ogle 2 (no known name)	"	——
Cem 15-LaPorte-Ind 1 (Morgan)	"	——
Cem 16-Will 2 (Braidwood-Oakwood)	"	——

sagittifolius drummondii (Lindl.) Shinners), pale Indian plantain (*Cacalia atriplicifolia* L.), wild hyacinth (*Camassia scilloides* (Raf.) Cory), spring beauty (*Claytonia virginica* L.), violet bush clover (*Lespedeza violacea* (L.) Pers.), early buttercup (*Ranunculus fascicularis* Muhl.), and starry campion (*Silene stellata* (L.) Ait). These were not found in prairie cemeteries (Betz and Lamp 1989).

It is interesting to note that savannas were not mentioned in the early papers of Mead (l846) and Brendel (l887). These silt-loam savanna cemteries are not the barrens of Mead since they contain only l8 species of the 77 non-woody species (23%) listed by Mead. Neither are they the copses of Brendel because these savanna cemeteries contain only 30 of the 97 non-woody species (30%) listed by him as occurring in copses. However, allowing for differences in geographical location, soil, and moisture relations, these savanna cemeteries appear to be similar to the oak savannas (oak openings) described by Curtis (1959) and Bray (1960).

Many of the prairie species found in these savanna cemeteries are the same ones characteristic of the "prairie matrix" used at Fermilab to restore prairie. These species are aggressive and able to invade and successfully dominate weedy communities in the early stages of prairie restoration (Betz l984). ·

Sand/gravel Complex Savanna (Cemetery 9)

Cemetery 9 (Bequaith Cemetery, Tazewell County, Illinois) was an unusual savanna cemetery. It was 0.4 ha (Table 1) with a soil designated as a Burkhart-Saude Sand/Gravel Complex (Table 3). The woody cover included bitternut hickory (*Carya cordiformis* (Wang) K.Koch) and black oak (*Quercus velutina* Lam.). It was neither a silt-loam nor a sand savanna. Rather, it appeared to be a combination of both. In addition to the dominant prairie grasses, such as big and little bluestems (*A. gerardii* Vitman, *A. scoparius* Michx.), Indian grass (*S. nutans* (L.) Nash), switch grass (*P. virgatum* L.), Scribner's panic grass (*P. oligosanthes scribnerianum* (Nash) Fern.), and porcupine grass (*Stipa spartea* Trin.), there were grasses more characteristic of open woods and savannas. These included Canadian wild rye (*Elymus canadensis* L.) and tall melic grass (*Melica nitens* Nutt.). Further, characteristic silt-loam prairie species, such as Bicknell's sedge (*Carex bicknellii* Britt.) and purple cone flower (*Echinacea pallida* Nutt.), grew together with a characteristic sand prairie species—clustered poppy mallow (*Callirhoe triangulata* (T. & G.) Gray). In addition, there were typical open woods and savanna species, such as pale Indian plantain (*Cacalia atriplicifolia* L.) and woodland sunflower (*Helianthus divaricatus* L.).

Sand Prairie (Cemetery l0)

Cemetery l0 (Springhill Cemetery, Whiteside County, Illinois) was the only sand prairie found during this study. It was approximately 0.8 ha and contained 53 species of prairie plants (Table 2). The soil was a Sparta sand (Table 3). Because it had a relatively deep A horizon (23-25 cm), it had a mixture of both silt-loam and sand prairie species. Some of the silt-loam prairie species were prairie dropseed grass (*Sporobolus heterolepis* Gray), cream wild indigo (*Baptisia leucophaea* Nutt.), Mead's sedge (*Carex meadii* Dew.), prairie coreopsis (*Coreopsis palmata* Nutt.), purple cone flower (*Echinacea pallida* Nutt.), hoary puccoon (*Lithospermum canescens* (Michx.) Lehm.), prairie cinquefoil (*Potentilla arguta* Pursh.), blue-eyed grass (*Sisyrinchium albidum* Raf.), and prairie violet (*Viola pedatifida* G.Don). Some of the sand prairie species were clustered poppy mallow (*Callirhoe triangulata* (T. & G.) Gray), hairy puccoon (*Lithospermum croceum* Fern), sand phlox (*Phlox pilosa* L.), purple milkwort (*Polygala polygama obtusata* Chodat), showy goldenrod (*Solidago speciosa* Nutt.), and hoary pea (*Tephrosia virginiana* (L.) Pers). A few sand weeds, such as western ragweed (*Ambrosia psilostachya coronopifolia* (T. & G.) Farw.), sand sedge (*Cyperus filiculmis* Vahl), and horse mint (*Monarda punctata villicaulis* Pennell) were also present.

Sand Savanna Prairies (Cemeteries ll-l6).

There are four major differences between the sand prairie and sand savanna cemeteries. First, the sand savanna cemeteries were associated with woody vegetation. Black oak (*Quercus velutina* Lam.) was the dominant tree; other woody species were black jack oak (*Q. marilandica* Muenchh.), red cedar (*Juniperus virginiana creber* Fern. & Grisc.), wafer ash (*Ptelea trifoliata* L.), fragrant sumac (*Rhus aromatica* Ait.), smooth sumac (*R glabra* L.), and sassafras (*Sassafras albidum* (Nutt.) Nees). Most of the trees observed were even aged and about l50 to 200 years old. It is probable that in presettlement times many, if not most, of these oaks were bushy, due to the recurrent annual fires that gave the landscape a prairie appearance. With the cessation of fires, such oak scrub could have grown up into open woodland, becoming the so-called black-oak savanna of today.

Second, the sand savannas had much shallower A layers than the sand prairie. The depth of the A horizon in these sand savanna cemeteries ranged from 5 to l0 cm compared with 23-25 cm in the sand prairie cemetery (Table 3).

Third, the sand savanna cemeteries had many more weedy sand species than the sand cemetery, due in part to patches of open sand. Some of these weedy species were beach wormwood (*Artemisia caudata* Michx.), narrow-leaved goosefoot (*Chenopodium lepotophyllum* Nutt.), purple love grass (*Eragrostis spectabilis* (Pursh) Steud.), large cottonweed (*Froelichia floridana campestris* (Small) Fern.), fall witch grass (*Leptoloma cognatum* (Schultes) Chase), sand primrose (*Oenothera rhombipetala* Nutt.), prickly pear cactus (*Opuntia humifusa* Raf)., slender knotweed (*Polygonum tenue* Michx.), and sand dropseed (*Sporobolus cryptandrus* (Torr.) Gray) (Table 2).

Fourth, while the total number of species found were approximately the same, the sand savanna cemeteries had fewer silt loam prairie species than the sand prairie cemetery. These include cream wild indigo (*Baptisia leucophaea* Nutt.), Mead's sedge (*Carex meadii* Dew.), purple cone flower (*Echinacea pallida* Nutt.), hoary puccoon (*Lithospermum canescens* (Michx.) Lehm.), and prairie dropseed (*Sporobolus heterolepis* Gray). On the other hand, there were some sand species that were found in the sand savanna cemeteries and not in the sand prairie cemetery. Some of these restricted sand species were sand milkweed (*Asclepias amplexicaulis* Sm.), sand coreopsis (*Coreopsis lanceolata* L.), slender bush clover (*Lespedeza virginica* (L.) Britt.), and hairy puccoon (*Lithoserpmum croceum* Fern.).

The dominant grass on these sand savanna prairies was little bluestem (*Andropogon scoparius* Michx.). Other prairie grasses present included big bluestem (*A. gerardii* Vitman), and Indian grass (*Sorghastrum nutans* (L.) Nash), along with certain sand species, such as Scribner's panic grass (*Panicum oligosanthes scribnerianum* (Nash) Fern.) and *P. villosissimum pseudopubescens* (Nash) Fern.).

Cemetery 16 (Braidwood-Oakwood-Will 2) was a large cemetery with a low, marshy area that supported a number of wet-prairie and marsh species. Some of these species were swamp milkweed (*Asclepias incarnata* L.), flat-top aster (*Aster umbellatus* Mill.), marsh marigold (*Caltha palustris* L.), marsh shield fern (*Dryopteris thelypteris pubescens* (Lawson) Nakai), royal fern (*Osmunda regalis spectabilis* Willd. Gray), and swamp saxifrage (*Saxifraga* pensylvanica L.). Because this savanna cemetery had both dune and swale vegetation, it was the richest in species composition of the six sand savanna cemeteries studied and had a total of 105 species.

These sand savannas were not mentioned either by Mead (1846) or Brendel (1887). However, they appear to be related to the oak barrens described by Curtis (1959).

Although these sand prairie and savanna cemeteries are small in size (Table 1), they are perhaps some of the best surviving remnants of presettlement sand prairies and savannas. Further, because these cemeteries still possess a valuable array of characteristic species, they can be used in evaluating the effectiveness of current restoration efforts for Illinois and Indiana savannas and prairies. In addition, the unplowed soils they possess provide a measure of the extent to which erosion has taken its toll in the surrounding fields. A number of these cemeteries, both in Illinois and in Indiana, have been designated as nature preserves. Further, these pioneer cemeteries give a small glimpse of what settlers viewed when they entered the wild Illinois-Indiana country in the early part of the nineteenth century.

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4/91

VEGETATION ANALYSIS OF A NATIVE HILLSIDE PRAIRIE WITHIN AN OAK WOODLAND IN SIOUX COUNTY, IOWA

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Abstract. From 1985 to 1989, a plant inventory of hill prairies and neighboring woods within Fairview Recreation Area, Sioux Country, Iowa, yielded 220 species in 63 families. In addition, a vegetation analysis was carried out in 1989 on west-facing, hillside prairie openings using a line transect technique. In the transect study, 40 vascular plants were recorded. The 20 species with the highest importance values included nine grasses, eight forbs, and three woody species. The three main families were Asteraceae (16 species), Poaceae (15 species), and Fabaceae (9 species). The primary genus was Aster with four species. The most frequent species were: *Aster laevis* (26), *Anemone patens* (21), *Medicago lupulina* (18), and *Calamovilfa longifolia* (15). Species with more western affinities, including *Astragalus missouriensis, Castilleja sessiliflora, Liatris punctate, Lithospermum incisum*, are found on these prairie openings.

INTRODUCTION

Although vegetation surveys of western Iowa have been taken over the past years, most of these have been checklists (Carter 1966, Novacek et al. 1985, Peck et al. 1984, Roosa et al. 1991, Vander Zee 1979.) Carter (1963) conducted a quadrat vegetation analysis on prairie hillsides along the Loess Hills, similar to the prairie hillsides in this study.

This study presents a flora and vegetation analysis of the Fairview Recreation Area, a 24.7 ha preserve under the management of the Sioux County Conservation Board. The preserve lies along the steep bluffs on the Big Sioux River in Sioux County, Iowa. These bluffs, at 458 m above sea level, support the woodland vegetation that marks the break between the river terraces and the uplands. The soil belongs to the Steimauer-Moody Association, which exhibits steep, well-drained, loamy, silty soils formed on glacial till and loess (Sioux County Soil Survey 1990).

The region experiences average winter temperatures of -7 C, average temperature of 20 C, average annual precipitation of 68 cm with 75% falling from April through September, and prevailing winds from the northwest (Sioux County Soil Survey 1990).

The study site lies within a predominantly oak woodland and consists of an irregular, 50-70 m, west-facing prairie corridor (Figure 1) bordered by bur oak (*Quercus macrocarpa* Michx.) on the hilltops and a variety of woody species along the deep ravines. The prairie site is on very steep, highly unstable soil. Miniature slumps are present, offering bare ground for opportunistic prairie species.

The county conservation board has expressed concern about the encroachment of competitive woody species onto the prairie openings, especially of bur oak, eastern red cedar (*Juniperus virginiana* L.), smooth sumac (*Rhus glabra* L.) and Virginia-creeper (*Parthemocissus quinquiefolia* (L.) Planch). Mutel (1989) referred to similar encroachment of woody species onto the prairie bluffs of the Loess Hills. This study was undertaken to document prairie species in woodland openings and to support possible future management decisions to control encroachment of competitive woody species.

Figure 1. West-facing prairie corridor.

METHODS

From 1985 to 1991, a checklist of the vascular vegetation was compiled. Plant specimen vouchers are located in herbarium cabinets at Northwestern College, Orange City, Iowa. The taxonomic nomenclature follows Great Plains Flora Association (1986) and Gleason and Cronquist (1963).

A 120-m, line transect analysis was made along the median of the prairie corridor in September 1989. A second, 20-m transect was taken on the steep, west-facing slope at a right angle to the corridor transect.

The Line Transect Technique (Cox 1967) includes several components for each species that the line intercepts: density, relative density, frequency, relative frequency, ground cover, relative ground cover, and importance value. The importance value represents the sum of the relative density, the relative frequency, and the relative ground cover for each species.

Color and black and white photos were taken of the study site. These photos record spring, summer, and fall settings from a fixed site.

RESULTS AND DISCUSSION

Two hundred and twenty species were found at the Fairview Recreation Area (Table 1). Eighty-four species were growing in the prairie study site.

The line transects intercepted 40 species: 15 forbs, 12 grasses, and 3 woody species. The top families were Asteraceae, 16, Poaceae, 15, and Fabaceae, 9. These top families had very close correlation to the same families, Poaceae 95, Asteraceae 88, and Fabaceae 34, included in a checklist of all flora in Lyon and Sioux counties (Peck et al. 1984). Table 2 includes the top 20 species listed in diminishing order of importance values.

The two top species demonstrated high importance values. The smooth blue aster, (*Aster laevis* L.) appeared to favor the edges of the miniature soil slumps. The pasque flower (*Anemone patens* L.) was found evenly distributed on the west-facing prairie slopes. Hegstad (1973) found the pasque flower in abundance on similar steep, west-facing slopes on loamy glacial till in northwestern North Dakota.

Black medic (*Medicago lupulina* L.) was third in importance value. This legume also capitalized on the bare, eroded soil of the small slumps.

The geographic location of the study site lends itself ecologically to interesting plant distribution limits. Gleason and Cronquist (1964) refer to the transition from the tallgrass prairie to the Eastern deciduous forest at Oak Grove Park in Sioux County, several miles south of the study site.

The 84 species found at the prairie study site have a certain percentage of species common to other studies in western Iowa. Percentage similarities are 88% in the Loess Hills (Novacek et al. 1985), 75% in Guthrie County (Roosa et al. 1991), 71% at Gitchie Manitou State Park (Vander Zee 1979), and 82% in northwestern North Dakota (Hegstad 1973).

Species of a more western affinity found at the study site were blazing star (*Liatrus punctata* Hook.), downy paintbrush (*Castilleja sessiliflora* Pursh.), dwarf wild indigo (*Amorpha nana* Nutt.), gray goldenrod (*Solidago nemoralis* Ait.), large beardtongue (*Penstemon grandiflorus* Nutt.), Missouri milkvetch (*Astragalus missouriensis* Nutt.), narrow-leaved puccoon (*Lithospermum incisum* Lehn.), sedge (*Carex helophila* Mack.), sneezewort aster (*Aster ptarmicoides* (Nees.) T. & G.), and white beard tongue, (*Penstemon albidus* Nutt.). Many of these are rare and/or endangered in Iowa. Two western species, evening star sand lily (*Mentzelia decapetala* (Pursch.) Urgan & Gilg.) and yucca (*Yucca glauca* Nutt.) were absent in the study site but are found along the Big Sioux River bluffs in nearby Plymouth County.

Table 1. The vascular flora of the Fairview Recreation Area.

Scientific name	*Common name*
EQUISETOPHYTA	
Equisetaceae	Horsetail family
Equisetum arvense L.	Common Horsetail
POLYPODIOPHYTA	
Ophioglossaceae	Adder's tongue family
Botrychium virginianum (L.) Sw.	Rattlesnake fern
PINOPHYTA	
Cupressaceae	Cypress family
Juniperus virginiana L.	Eastern red cedar
MAGOLIOPHYTA: MAGNOLIATAE	
Aceraceae	Maple family
Acer negundo L.	Box-elder
Anacardiaceae	Cashew family
Rhus glabra L.	Smooth sumac
Toxicodendron radicans (L.) Kuntz	Poison ivy
Apiaceae	Parsley family
Lomatium oreintale C. & R.	
Ozmorhiza claytonii (Michx.) Clarke	Sweet cicley
Sanicula marilandica L.	Black snake root
Thaspium barbinode (Michx.) Nutt.	Meadlow parsnip
Apocynaceae	Dogbane family
Apocynum cannabinum L.	Indian hemp
Aralia nudicaulis L.	Wild sarsparilla
Aclepidaceae	Milkweed family
Asclepias syriaca L.	Common milkweed
Asclepias verticillata L.	Whorled milkweed
Asclepias viridiflora Raf.	Green milkweed
Asteraceae	Aster family
Achillea millefolium L.	Common yarrow
Ambrosia artemisiifolia L.	Small ragweed
Ambrosia trifida L.	Giant ragweed
Anthemis cotula L.	Dog fennel
Artemisia ludovicianna Nutt.	Prairie sage
Aster eriocoides L.	Heath aster
Aster laevis L.	Smooth aster
Aster oblongifolius Nutt.	Aromatic aster
Aster ptarmicoides (Nees) T. & G.	Sneezewort aster
Aster sericeus Vent.	Silky aster
Bidens cernua L.	Stick-tight
Bidens frondosa L.	Beggar's ticks
Carduus acanthoides L.	Erect musk thistle
Cirsium flodmanii (Rybd.) Arthur	Dog thistle
Conyza canadensis (L.) Cron.	Horseweed
Coreopsis palmata Nutt.	Tickseed
Dyssodia papposa (Vent.) Hitchc.	Fetid marigold
Echinacea angustifolia DC.	Purple coneflower

Table 1. Continued

Scientific name	*Common name*
Asteraceae, continued	Aster family
Erigeron philadephicus L.	Common fleabane
Erigeron strigosus Muhl.	Daisy fleabane
Eupatorium rugosum Houtt.	White snakeroot
Grindelia squarrosa (Pursh) Dunal	Gum plant
Helianthus annuus L.	Common sunflower
Helianthus rigidus (Cass.) Desf.	Beautiful sunflower
Helianthus maximiliani Schrad.	Maximilian sunflower
Kuhnia eupatoriodes L.	False-bonset
Lactuca biennis (Moench) Fern.	Wild lettuce
Lactuca pulchella (Pursh) DC.	Wild lettuce
Lactuca serriolla L.	Prickly lettuce
Liatrus aspera Michx.	Rough blazing star
Liatrus punctata Hook.	Dotted blazing star
Prenanthes alba L.	White rattlesnake-root
Ratibida pinnata (Vent.) Barng.	Prairie coneflower
Senecio plattensis Nutt.	Prairie ragwort
Soldiago nemoralis Ait.	Gray goldenrod
Soldiago rigida L.	Stiff goldenrod
Taraxacum officianale Weber	Common dandelion
Tragopogon dubius Scop.	Goat's beard
Veronica fasciculata Michx.	Bunched ironweed
Betulaceae	Birch family
Ostrya virginiana (Mill.) K. Koch	Hop Hornbeam
Boraginaceae	Borage family
Lappula redowskii (Hornem.) Greene	Stickseed
Lithospermum canescens (Michx.) Lehm.	Hoary puccoon
Lithospermum incisum Lehm.	Narrow-leaved puccoon
Onosmodium occidentale Mack.	False gromwell
Brassicaiceae	Mustard family
Erysimum cheiranthoides L.	Wormseed mustard
Rorippa islandica (Oeder) Borbas.	Yellow marsh cress
Cannabinaceae	Hemp family
Cannabis sativa L.	Hemp
Caprifoliaceae	Honeysuckle family
Lonicera tatarica L.	Tatarian honeysuckle
Symphoricarpos occidentalis Hoek.	Wolfberry
Viburnum lentago L.	Nannyberry
Caryophyllaceae	Pink family
Cerastium viscosum L.	Mouse-ear chickweed
Silene stellata (L.) Ait.	Starry campion
Celastraceae	Bittersweet family
Celastrus scandens L.	Bittersweet
Euonymus atropurpureus Jacq.	Wahoo
Chenopodiaceae	Goosefoot family
Chenopodium fremontii Wats.	Small-leaved goose foot
Chenopodiaceae, continued	Goosefoot family
Chenopodium hybridum L.	Maple-leaved goose foot
Convolvulaceae	Morning-glory family
Convolvulus sepium L.	Wild morning-glory
Cornaceae	Dogwood family
Cornus drummondii Mey.	Rough-leaved dog wood
Cucurbitaceae	
Echinocystis lobata (Michx.) T. & G.	Wild cucumber
Euphorbiaceae	Spurge family
Euphorbia dentata Michx.	Toothed spurge
Euphoriba glyptosperma Englem.	Spurge
Euphorbia marginata Pursh	Snow-on-the-mountain
Fabaceae	Bean family
Amorpha canescens Pursh	Lead plant
Amorpha fruticosa L.	Wild false indigo
Amorpha nana Nutt.	Fragrant false indigo
Amphicarpa bracteata (L.) Fern.	Hog-peanut
Astragalus crassicarpus Nutt.	Ground-plum
Astragalus missouriensis Nutt.	Missouri milkvetch
Cassia fasciculata Michx.	Partridge pea
Desmodium canadense (L.) DC.	Tick-clover
Glycyrrhiza lepidota (Nutt.) Pursh	Wild licorice
Medicago lupulina L.	Black medic
Melilotus alba Desr.	White sweet clover
Melilotus officianalis (L.) Lam.	Yellow sweet clover
Petalostemum candidum (Willd.) Michx.	White prairie clover
Petalostemum purpureum (Vent.) Rybd.	Purple prairie clover
Psoralea esculenta Pursh	Indian breadroot
Trifolium hybridum L.	Alsike clover
Trifolium pratense L.	Red clover
Trifolium repens L.	White clover
Fagaceae	Beech family
Quercus macrocarpa Michx.	Bur oak
Fumariaceae	Fumitory family
Dicentra cucullaria (L.) Bernh.	Dutchman's breeches
Hydrophyllaceae	Waterleaf family
Ellisia nyctelea L.	Waterpod
Hydrophyllum virginianum L.	John's cabbage
Juglandaceae	Walnut family
Juglans nigra L.	Black walnut
Lamiaceae	Mint family
Leonuris cardiaca L.	Motherwort
Nepeta cataria L.	Catnip
Scutellaria parvula Michx.	Small skullcap

Table 1. Continued

Scientific name	*Common name*
Linaceae	Flax family
Linum rigidum Pursh	Yellow flax
Lobeliaceae	Lobelia family
Lobelia siphilitica L.	Blue lobelia
Menispermaceae	Moonseed family
Menispermum canadense L.	Moonseed
Nyctaginaceae	Four o'clock family
*Mirabilis hirsuta (*Pursh) MacM.	Hairy four o'clock
Mirabilis nyctaginea (Michx.) MacM.	Wild four o'clock
Oleaceae	Olive family
Fraxinus pennsylvania Marsh.	Green ash
Onagraceae	Evening primrose family
Oenothera biennis L.	Evening primrose
Oenothera serrulata Nutt.	Toothed evening primrose
Oxalidaceae	Wood-sorrel family
Oxalis stricta L.	Yellow wood-sorrel
Papaveraceae	Poppy family
Sanguinaria canadense L.	Bloodroot
Plantaginaceae	Plantain family
Plantago major L.	Common plantain
Polygalaceae	Milkwort family
Polygala alba Nutt.	Milkwort
Polygonaceae	Buckwheat family
Polygonum aviculare L.	Knotweed
Polygonum convolvulus L.	Black bindweed
Polygonum erectum L.	Erect knotweed
Polygonum pensylvanicum L.	Pinkweed
Rumex crispus L.	Curly Dock
Ranunculaceae	Buttercup family
Anemone canadensis L.	Meadow anemone
Anemone cylindrica Gray	Thimbleweed
Anemone patens L.	Pasque flower
Aquilegia canadensis L.	Columbine
Delphinium virescens Nutt.	Prairie larkspur
Ranunculus abortivus L.	Small-flowered crowfoot
Thalictrum dasycarpum Fisch. & Lall	Meadow-rue
Rhamnaceae	Buckthorn family
Ceanothus americanus L.	New Jersey tea
Rahmnus frangula L.	Buckthorn
Rosaceae	Rose family
Amelanchier sanquinea (Pursch) DC.	Red shadbush
Fragaria virginiana Dcne.	Wild strawberry
Geum laciniatum Murr.	Rough avens
Rosaceae, continued	Rose family
Potentilla norvegica L.	Rough cinquefoil
Prunus americana Marsh.	Wild plum
Prunus virginiana L.	Choke cherry
Rosa suffulta Greene	Prairie rose
Rubus occidentalis L.	Black raspberry
Rubiaceae	Madder family
Galium aparine L.	Cleavers
Galium triflorum Michx.	Sweet-scented bedstraw
Rutaceae	Rue family
Zanthoxylum americanum Mill.	Prickly Ash
Salicaceae	Willow family
Populus deltoides Marsh.	Eastern cottonwood
Salix amygdaloides Anderss.	Peach-leaved willow
Salix interior Rowlee	Sandbar willow
Santalaceae	Sandalwood family
Commandra umbellata (L.) Nutt.	Bastard toadflax
Saxifragaceae	Saxifrage family
Heuchera richardsonini R. Br.	Alum root
Ribes missouriense Nutt.	Wild gooseberry
Scrophulariaceae	Figwort family
Castilleja sessiliflora Pursh	Downy painted-cup
Penstemon albidus Nutt.	White prairie beard-tongue
Penstemon grandiflorus Nutt.	Giant blue beard-tongue
Verbascum thaspus L.	Common mullein
Solanaceae	Tomato family
Physalis heterophylla Ness	Ground cherry
Tiliaceae	Basswood family
Tilia americana L.	Basswood
Ulmaceae	Elm family
Celtis occidentalis L.	Hackberry
Ulmus americana L.	American elm
Ulmus pumila L.	Dwarf elm
Ulmus rubra Muhl.	Slippery elm
Urticaceae	Nettle family
*Laportea canadense (*L.) Wedd.	Wood nettle
Parietaria pensylvanica Muhl.	Pellitory
Urtica dioica L.	Stinging nettle
Verbenaceae	Vervain family
Verbena bracteata Lag. & Rodr.	Bracted vervain
Verbena stricta Vent.	Hoary vervain
Verbena urticifolia L.	White vervain
Violaceae	Violet family
Viola papilionacea Pursh	Common blue violet
Viola pedatifida G. Don.	Prairie violet
Viola pubescens Ait.	Smooth yellow violet

Table 1. Continued

Scientific name	*Common name*
Vitaceae	Grape family
Parthenocissus quinquefolia (L.) Planch.	Virginia creeper
Vitis riparia Michx.	Riverbank grape
MAGNOLIOPHYTA: LILIATAE	
Cyperaceae	Sedge family
Carex blanda Dew.	Woodland sedge
Carex gravida Bailey	Heavy sedge
Carex heliophila Mark.	
Carex sprengelii Dewey	Sprengel's sedge
Cyperus exculentus L.	Yellow nutsedge
Scirpus atrovirens Willd.	Dark green bulrush
Iridaceae	Iris family
Sisyrinchium campestre Bickn.	Great Plains blue-eyed grass
Lemnaceae	Duckweed family
Lemna minor L.	Duckweed
Liliaceae	Lily family
Smilacina stellata (L.) Desf.	Small false solomon's-seal
Trillium nivale Riddell	Snow trillium
Poaceae	Grass family
Agropyron repens (L.) Beauv.	Quack grass
Agropyron trachycaulum (Link) Steud.	Wheat grass
Agrostis alba L.	Redtop
Agrostis hyemalis (Walt.) BSP	Tickle grass
Agrostis perennans (Walt.) Tuckerm	Upland bent
Andropogon gerardi Vitman	Big bluestem
Andropogon scoparius Michx.	Little bluestem
Bouteloua curtipendula (Michx.) Torr.	Side-oats gramma
Bromus inermis Leyss.	Hungarian brome
Bromus japonicus Thunb.	Japanese chess
Bromus tectorum L.	Downy chess
Calamovilfa longifolia (Hook.) Scribn.	
Echinochloa crus-galli (L.) Beauv.	Barnyard grass

Table 1. Continued

Scientific name	*Common name*
Poaceae (continued)	Grass family
Elymus canadensis L.	Wild rye
Elymus villosus Muhl.	
Elymus virginicus L.	Virginia wild rye
Eragrostis cilianensis (All.) Link	Stink grass
Eragrostis pectinacea (Michx.) Nees.	Carolina love grass
Eragrostis spectabilis (Pursh) Steud.	Petticoat climber
Hordeum jubatum L.	Squirreltail grass
Leersia oryzoides (L.) Sw.	Rice cut grass
Leersia virginica Willd.	White grass
Muhlenbergia cuspidata (Torr.) Rybd.	
Muhlenbergia racemosa (Michx.) BSP	Mountain wild rice
Muhlenbergia schreberi J.F. Gunel	
Panicum capillare L.	Witch grass
Panicum leibergii (Vasey) Scribn.	Leibig's panicum
Panicum oligosanthes Schutt.	Few-flowered panicum
Panicum virgatum L.	Switch grass
Phleum pratense L.	Timothy grass
Phragmites australis (Cav.) Steud.	Reed grass
Poa compressa L.	Canadian bluegrass
Poa pratensis L.	Kentucky bluegrass
Setaria viridis (L.) Beauv.	Green foxtail
Sorghastrum nutans (L.) Nash	Indian grass
Sporobolus heterolepis Gray	Prairie dropseed
Stipa spartea Trin.	Porcupine grass
Pontederiaceae	Pickerelweed family
Heteranthera dubia (Jacq.) MacM.	Water star-grass
Potemogetonaceae	Pondweed family
Potemogeton foliosus Raf.	Leafy pondweed
Smilacaceae	Greenbrier family
Smilax ecirrhata (Engelm.) S. Wats	Greenbrier
Smilax herbacea L.	Carrion flower
Typhaceae	Cattail family
Typha latifolia L.	Wide-leaved cattail

Table 2. Importance values for the 20 highest ranking species.

Common name	*Latin name*	*Importance value*
Smooth blue aster	*Aster laevis* L.	25.7
Pasque flower	*Anemone patens* L	20.8
Black medic	*Medicago lupulina* L..	18.2
Big sandgrass	*Calamovilfa longifolia* (Hook.) Scribn.	15.5
Virginia-creeper	*Parthenocissus quinquefolia* (Knerr) Hitchc.	12.3
Kentucky bluegrass	*Poa pratensis* L.	12.2
Stiff sunflower	*Helianthus rigidus* (Cass.) Desf.	11.8
Porcupine grass	*Stipa spartea* Trin.	9.4
Indian grass	*Sorghastrum avenaceum* (Michx.) Nash	8.9
Toadflax	*Comandra umbellata* (L.) Nutt.	8.7
Big bluestem	*Andropogon gerardi* Vitman	8.5
Goatsbeard	*Tragopogon dubius* Scop.	8.5
Prairie dropseed	*Sporobolus heterolepsi* (Gray) Gray	8.4
Purple coneflower	*Echinacea angustifolia* DC.	6.8
Plains muhly	*Muhlenbergia cuspidata* (Torr.) Rybd.	6.4
Bur oak	*Quercus macrocarpa* Michx.	6.3
Small panicgrass	*Panicum oligosanthes* Schult.	5.7
Little bluestem	*Andropogon scoparius* Michx.	5.6
Western snowberry	*Symphoricarpos occidentalis* Hook.	5.6
Sneezewort aster	*Aster ptarmicoides* (Nees.) T. & G.	5.6

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WETLANDS: RESERVOIRS FOR PRAIRIE BIOTA IN "PRAIRIELESS" LANDSCAPES

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Abstract. Much of the eastern tallgrass prairie region has seemingly lost its prairie heritage. Natural areas inventories in Iowa and Illinois have discovered only scattered, small remnants in vast areas formerly dominated by prairie. Recent inventories Illinois' Fox River valley have catalogued the plants and animals of remnant natural areas. This rich agricultural region has few prairies—all small and isolated. However, sedge meadows and fens are numerous and together form large wetland ecosystems. These two communities are biologically very similar to the lowland prairies in Illinois. Approximately 50% of the fen flora consists of prairie plants. Twelve butterfly, five herpetile, and three bird species characteristic of lowland prairies consistently occupy sedge meadows. These data suggest that a significant component of the prairie biota lies "hidden" in the wetlands of the "prairieless" landscapes. In such areas, restoration can be most effective if large lowland prairies are reconstructed adjacent to remnant wetlands.

INTRODUCTION

Conservationists have long lamented the demise of the eastern tallgrass prairie. The conversion of Transeau's Prairie Peninsula into the world's most productive farmland was so complete that most of this sea of grass is but a memory etched in the diaries of early travellers.

Statewide natural areas inventories have documented the prairie's destruction. Less than 0.01% of the original tallgrass prairie remains in Illinois, the Prairie State (White 1978). Similar estimates have been made for Wisconsin (Curtis 1959) and Iowa (Roosa 1978). The majority of known remnants are small and isolated. A few notable exceptions include the Loess Hills and the Little Sioux River watershed of western Iowa and the sandy plain of the ancient glacial Lake Chicago. The latter area borders Lake Michigan in three states. Excluding these landforms and similar areas of steep topography or sandy soil, most of the midwestern heartland is now a prairieless landscape, except for the unique Flint Hills of Kansas.

In many prairieless regions of the Midwest, remnant wetlands are frequent, often large, and either clustered or interconnected. Examples include the upper Fox River valley of northeastern Illinois (Schennum 1989, White 1978), the Iowan Surface landform of northeastern Iowa (Schennum 1986), and the Kettle Moraine country of southeastern Wisconsin (Germain 1977). Abundant sedge meadow and fen communities, ecologically similar to lowland prairie, could serve as reservoirs of prairie biota in these areas. The restoration of lowland prairie communities adjacent to these wetlands could allow the spread of many prairie elements into the reconstructed prairies, re-creating a large fraction of the once common prairie-wetland ecosystems of these otherwise prairieless regions.

The purpose of this paper is to test these hypotheses with data from several of the McHenry County Conservation District's surveys of wetland flora and fauna. Summarized data from other similar studies also are presented. Courses of action in wetland and prairie management and restoration suggested by these data are then proposed.

METHODS AND RESULTS

The natural resource management staff of the McHenry County Conservation District (MCCD) has been conducting biological inventories in several wetlands of the upper Fox River valley for the past five years.

The results of MCCD plant inventories in five large sedge meadow/fen ecosystems in the upper Fox River watershed are shown in Table 1. A total of 71 species of wet to wet-mesic prairie plants occur in these wetland communities and associated small pockets of wet old fields (formerly cultivated wet prairie). In at least four of the five sites, 39 of the 71 (55%) prairie species are present. In at least three of the five sites, 55 of the 71 (77%) prairie species are present. This compositional overlap also has been reported in sedge meadows and fens of adjacent southern Wisconsin. In sampling several stands in prairies and wetlands there, Curtis (1959) found an index of similarity of 54 between wet prairies and fens and 46 between wet prairies and sedge meadows.

The results of District faunistic inventories for six large Fox River valley wetlands are given in Table 2. A total of 12 habitat-restricted butterflies characteristic of wet to mesic prairie (see Panzer 1984) were found in the sedge meadows and fens of these six wetlands (top of Table 2). Five of the six wetlands supported 6, or 50%, of the 12 prairie species. Three of the six wetlands supported 9, or 75%, of the prairie butterflies.

The results of herpetological surveys on the same six major wetlands are shown in the middle of Table 2 (data from Mierzwa 1989, 1990). His field work indicated that a group of five prairie-associated species (leopard frog, *Rana pipiens*, data yet to be completely gathered) consistently occur in the sedge meadows at these sites. The green snake (*Opheodrys vernalis*), a true prairie indicator species (Smith 1961), occurs in five of the six sites, as do two savanna grassland species, the DeKay's and eastern garter snakes (*Storeria dekayi* and *Thamnophis sirtalis*).

The bottom of Table 2 displays the results of MCCD bird surveys for five of the six wetlands (Oakwood Hills Fen has not yet been surveyed). Although five bird species from field census records are prairie species, the sedge wren (*Cistothorus platensis*) is the only true low-prairie nester (Bohlen 1989) found consistently in sedge meadows. Sandhill cranes (*Grus canadensis*) and swamp sparrows (*Melospiza georgiana*) were consistently recorded in these wetlands, but they are true wetland, not prairie, inhabitants (Bohlen 1989). Their inclusion here as prairie birds refers more to their probable occasional use of prairie habitats for feeding. The eastern meadowlark (*Sturnella magna*) and the bob-o-link (*Dolichonyx oryzivorus*), two well-known lowland prairie inhabitants, were seldom found to utilize sedge meadows in any manner.

Several other studies by scientists and local naturalists have contributed to the wealth of biological knowledge on these sites. Among them have been the Illinois Natural Areas Inventory (INAI) of 1976-77 summarized by White (1978), the 1986-1991 Breeding Bird Atlas project of the Illinois Department of Conservation (Kleen 1986), and Ron Panzer's studies of insects at Spring Hill Farm Fen (Panzer and Stillwaugh 1986). These studies generally support the hypothesis that the sedge meadows and fens of this "prairieless" landscape support a sizable portion of the lowland prairie flora and fauna. For example, Moran (1981), in a review of the INAI floristic database for 12 fens (11 in the upper Fox River valley), found that of the 36 prevalent species on 10 of the sites, 20 (or 56%) are characteristic of wet to mesic prairie (see Swink and

Table 1. Prairie plants of Fox River valley wetlands.

	Site				
Species	*Alden Sedge Meadow*	*Oakwood Hills Fen*	*Lyons Prairie Marsh*	*Hickory Grove Fen*	*Green Wood Fen*
Allium cernuum		x			x
Andropogon gerardi	x	x	x	x	x
Anemone canadensis	x			x	x
Apios americana	x	x	x	x	x
Aster lateriflorus	x	x		x	
Aster novae-angliae	x	x		x	x
Aster simplex	x	x	x	x	x
Calamagrostis canadensis	x	x	x	x	x
Carex buxbaumii	x	x	x		x
Carex lanuginosa	x	x	x		x
Carex tetanica	x	x	x	x	
Cicuta maculata		x	x	x	x
Commandra richardsiana		x		x	
Cypripedium candidum		x			
Demodium canadense	x				
Dodecatheon meadii		x			x
Dryopteris thelypteris	x	x	x	x	x
Elymus virginicus	x	x	x	x	x
Galium boreale	x	x		x	x
Galium obtusum	x	x	x	x	
Gentiana andrewsii	x	x			
Gerardia tenuinfolia	x	x			
Helenium autumnale	x	x	x		
Helianthus grosseserratus	x	x	x	x	x
Heliopsis helianthoides	x	x		x	x
Heuchera richardsonii	x			x	
Hypoxis hirsuta	x	x		x	x
Iris virginica	x	x	x	x	x
Lathyrus palustris	x	x	x	x	x
Liatris spicata		x	x	x	x
Lilium michiganense	x			x	x
Lycopus americanus	x		x	x	x
Lysimachia quadriflora	x	x	x	x	x
Lythrum alatum	x	x	x	x	x
Monarda fistulosa	x	x		x	x
Oxypolis rigidior	x	x	x	x	x
Pedicularis canadensis		x			
Pedicularis lanceolata	x	x	x	x	x
Phlox glaberrima	x				
Phlox pilosa	x	x		x	x
Physostegia virginiana			x	x	x
Pycnanthemum virginianum		x	x	x	x
Ratibida pinnata	x			x	x
Rosa blanda	x			x	
Rudbeckia hirta	x	x	x	x	x
Salix gracilis	x	x	x		x
Saxifraga pensylvanica	x				x
Schizacrium scoparium		x			
Senecio pauperculus balsamitae	x	x		x	x
Silphium integrifolium		x		x	x
Silphium perfoliatum		x		x	x
Silphium terebinthinaceum		x		x	
Sisyrinchium albidum	x			x	x
Smilacina stellata	x	x	x	x	x
Solidago gigantea	x	x	x	x	x
Solidago riddellii	x	x	x	x	x
Sorghastrum nutans	x	x			x
Spartina pectinata	x	x		x	x
Spiraea cernua	x	x		x	
Sporobolus heterolepsis	x		x		
Thalictrum dasycarpum	x	x	x	x	x
Thalictrum revolutum	x				
Tradescantia ohiensis		x		x	x
Valeriana ciliata	x	x	x		x
Verbena hastata	x		x	x	x
Vernonia fasciculata			x	x	x
Veronicastrum virginicum	x			x	x
Zizia aurea	x	x			

Table 2. Prairie animals of Fox River valley wetlands.

Species	*Alden Sedge Meadow*	*Lyons Prairie Marsh*	*Eliza-Beth Lake*	*Spring Hill Farm Fen*	*Hickory Grove*	*Oakwood Hills Fen*
Butterflies						
Long dash	x	x		x		x
Black dash	x	x	x	x	x	x
Delaware skipper	x	x		x	x	x
Coral hairstreak				x		
Acadian hairstreak	x	x		x		
Purplish cooper	x		x			
Sivery checkerspot				x		
Great Spangled fritillary	x	x	x	x	x	x
Aprhodite	x		x	x	x	x
Silver-bordered fritillary	x	x	x	x	x	x
Common wood nymph	x	x	x	x	x	x
Northern eyed brown	x	x	x	x	x	x
Reptiles and amphibians						
Leopard frog	?	?	x	x	?	
Blanding's turtle	x	x	x	x		
Western smooth green snake	x		x	x	x	
Eastern garter snake	x	x	x	x	x	x
Dekays' snake	x	x	x	x		x
Birds						
Sandhill crane		x	x			
Sedge wren		x	x		x	
Bob-o-link					x?	
Eastern meadow lark	x			x?		
Swamp sparrow	x	x	x	x	x	

Wilhelm 1979 for community associations of plants). In his narrative, Moran specifically noted the floristic overlap between these prairie types and fens. Panzer and Stillwaugh (1986) found 10 species of butterflies at Spring Hill Farm Fen which are characteristic of wet and/or mesic prairie (see Opler and Krizek 1984 for community associations of butterflies).

DISCUSSION

The District database for upper Fox River valley wetlands of northeastern Illinois demonstrates that sedge meadow/fen community complexes are significant reservoirs of lowland prairie flora and fauna. This is especially true for vascular plants, butterflies, and herpetiles. The studies by Curtis (1959) (in adjacent southern Wisconsin), Moran (1981), and Panzer and Stillwaugh (1986), discussed previously, lend further support to this hypothesis. The modern ecological theory that species and communities are distributed in a continuum along environmental gradients (Greig-Smith 1983) would predict this overlap in species composition. The soil moisture needs of the prairie plants and specific larval food plant requirements of the butterflies are met in both sedge meadows/fens and lowland prairies. The similarity in habitat structure, food resources, soil moisture, and other niche parameters similarly allows several herpetiles to survive in either community.

Many wet to mesic prairie species from these three major taxonomic groups apparently are absent from Fox River valley wetlands. Several prairie legumes and some composites are never found in the region's fens (Moran 1981). The two-spotted skipper (*Euphyes bimacula*), meadow fritillary (*Boloria bellona*), and regal fritillary (*Speyeria idalia*) are missing from the present surveys and are seldom reported elsewhere in the region (Panzer, personal communication). Literature descriptions of their habitats include wetland and/or wet prairies (Opler and Krizek 1984, Ebner 1970). The plains garter snake (*Thamnophis radix*) and rare massasauga rattlesnake (*Sistrurus catenatus*) are conspicuously absent from MCCD herpetological studies despite their reported association with wet prairie habitats (Smith 1961, Dalrymple and Reichenbach 1981). The absence of many plant species from sedge meadow/fens may be due to their intolerance for saturated peat/muck substrates. The lack of slightly better-drained mesic prairie communities in the immediate vicinity of sedge meadow and fen remnants may explain the absence of some expected butterflies (Panzer 1989) and reptiles (Mierzwa 1988, Bushey 1978).

The scarcity of prairie birds in the Fox River valley wetland surveys is not unexpected because most prairie species, like some of the "missing" butterflies and snakes, prefer upland mesic or dry prairie, or grasslands with shorter and/or sparser cover (Bohlen 1989, Byre 1989, Birkenholz 1973). However, both eastern meadowlarks and bob-o-links prefer rich prairies with tall, dense vegetation (Birkenholz 1973) structurally similar to fens and sedge meadows. Their absence is due probably to competition, as other passerine bird species may utilize lowland grass/sedge dominated meadows more efficiently (Weller 1981). Sedge wrens and swamp sparrows, frequent in Fox River valley sedge meadows, are probably examples of these competitors, as are redwings (not reported here but common in District surveys). Byre (1989) contends that meadow-nesting redwings are displacing bob-o-links from suitable nesting habitat. The implications of this information for grassland-wetland preservation, management, and reconstruction are quite significant. In "prairieless" regions like the upper Fox River valley of northeastern Illinois, the biological potential of prairie ecosytems conservation can be maximized best by making the following three actions of highest priority. First, make every effort to ensure the permanent preservation and proper management of remnant wetlands. Sedge meadow/fen community complexes are especially important because they harbor many prairie plants and animals.

Second, protect and restore large expanses of underdeveloped, disturbed, open land adjacent to and between these remnant wetland communities, not just as a buffer, but as areas into which the wetland communities can expand. This is particularly significant given the importance of habitat size and continuity shown by the application of classic island biogeographic principles to mainland "island" natural areas (Samson 1983, Panzer 1985)

Finally, where soil and hydrological conditions indicate that prairie restoration is appropriate, this contiguous and intervening disturbed land should be restored to lowland wet to mesic prairie to re-create presettlement prairie-wetland ecosystem complexes. Low vagility species groups, such as the many prairie vascular plants, habitat-restricted insects, and reptiles discussed here, "hidden" in the adjacent remnant wetland can then more easily colonize the restored prairies, making them more complete communities. It is unlikely that such species will colonize an isolated prairie restoration and survive.

Panzer and Stillwaugh (1988), in their three-year study of the insects of the 243-ha (600-acre) Fermi Lab Prairie Restoration, have shown that low vagility, habitat-restricted prairie insects probably are not recolonizing this 20-year-old, large, isolated prairie, reconstructed on former cropland. In fact, half of the 27 habitat-restricted insects recorded here are wetland species that probably colonized the prairie restoration from the tiny remnant wetlands present. The other easily could have come from adjacent forest edge habitats.

The McHenry County Conservation District has undertaken the monumental tasks outlined in the three steps above. During its 19-year existence as an open-space/natural areas protection agency, it has preserved several high quality (minimally disturbed) wetlands in the upper Fox River valley. Abundant disturbed land contiguous to these natural areas has been protected also. In 1985, the District formulated a novel land-management policy which commits the organization to long-term restoration of all its minimally developed properties to presettlement (1830-1840) ecosystems. Consequently, the District's Natural Resource Management Department has been managing its high quality wetlands with carefully timed prescribed burning, brush removal, and purple loosestrife control. Contiguous disturbed lands are managed similarly to encourage the expansion and connection of wetland communities. Where these disturbed lands are formerly cultivated or overgrazed lowland prairie, reconstruction of the latter community is being undertaken to reestablish the presettlement prairie-wetland matrices with maximum floral and faunal diversity. The following two examples of MCCD site management plans will illustrate these processes.

The 294-ha (725-acre) Lyons Prairie and March-Hickory Grove Conservation Area in southeast McHenry County was once a quilt of interwoven marshes and ponds, sedge meadows, fens, and wet to mesic prairies, all bordered by rolling upland savannas. As shown in Figure 1, the marshes and ponds remain, as do several of the sedge meadows and fens, some bordered by very tiny vestiges of prairie. Virtually all of the lowland prairie and some intermixed sedge meadow were drained artificially and farmed. These areas are now Eurasian grass meadows and old fields. The site plan calls for drain tile blockage and extensive restoration of these disturbed areas, creating a mile-long continuum of wetlands and lowland prairie. As shown in Tables 1 and 2, many prairie elements are present in the remnant sedge meadows. With the creation of adjacent lowland prairie, many of the prairie plants and animals that cannot or will not be reintroduced may colonize the restorations, making them more complete biological systems.

At Glacial Park in northeast McHenry County, MCCD is engaged in a restoration of even grander proportions. This 1,013-ha (255-acre) property was ecologically scalped by intensive grazing and row-crop agriculture. Left behind was a cluster of rugged glacial hills cloaked in degraded savannas and planted hay meadows, over-

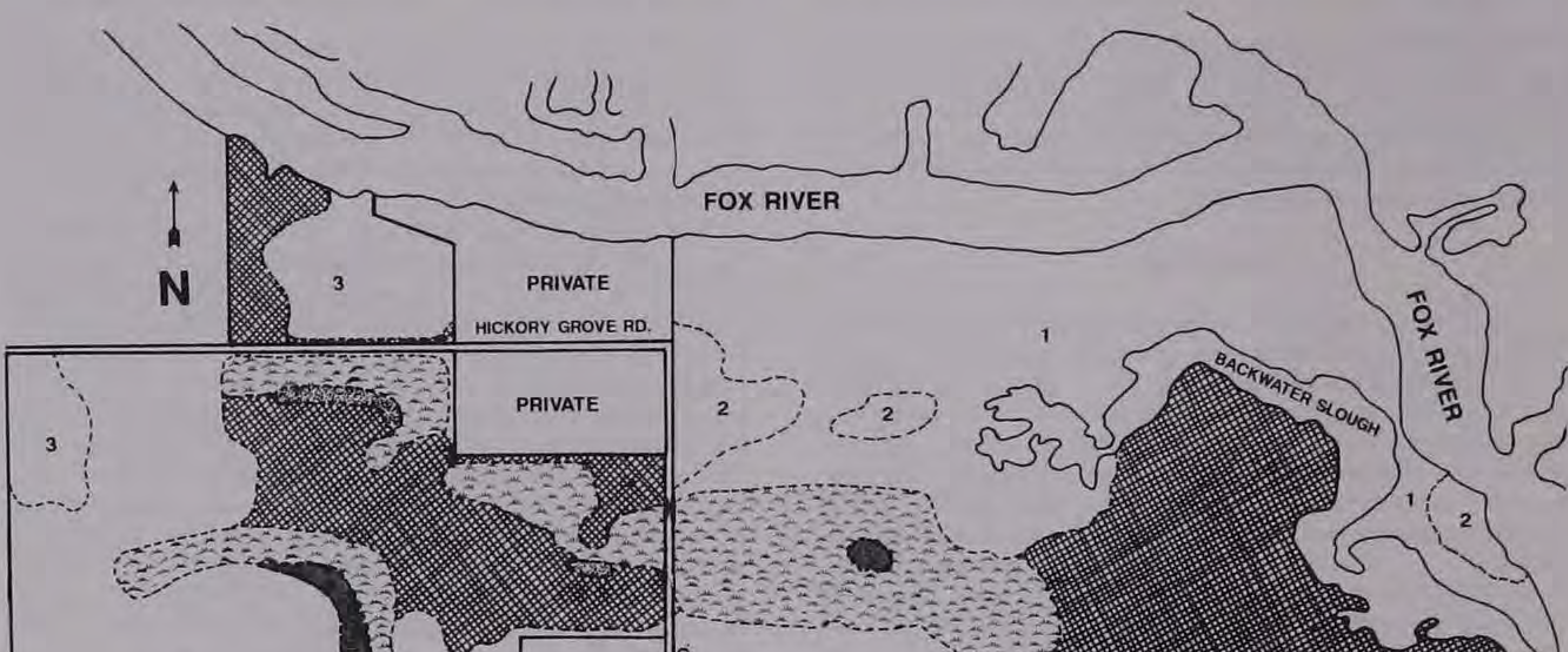

Figure 1. Lyons Prairie & Marsh/Hickory Grove Management Plan Map.

looking the broad valley of Nippersink Creek, a major tributary of the Fox River. Scattered in this artificially drained agricultural valley are small, remnant sedge meadows and even a few tiny strips of railroad right-of-way prairie (see Figure 2). Although the Glacial Park wetland remnants are not included in Tables 1 and 2, District inventories have discovered much of the same prairie flora and fauna in these areas. Initial management efforts have concentrated on structural restoration of these valley sedge meadows, using mechanical brush removal and prescribed burning. In addition, the old field adjacent to the easternmost wetland has been sown with prairie seed to provide expanded lowland prairie habitat for the prairie flora and fauna still present. A second step will be to develop a continuous wetland-prairie matrix along Nippersink Creek by restoring wet prairies and sedge meadows on the present Eurasian grass meadows between the remnant wetlands (see Figure 2).

The grander scale of this project is described in a two-year study on the feasibility of reconstructing a very large natural grassland in McHenry County (MCCD 1987, Schennum, et al. 1988). That study concluded that the Nippersink Valley at Glacial Park was an ideal location to restore a 1,000-acre prairie. Recently, the District made this dream a reality by purchasing the Wildberry Farm, that contains much of the valley adjacent to older MCCD holdings. When the existing leases on this farm expire in three years, the District will undertake the awesome task of reconstructing the entire milieu of wetlands, lowland prairies, and upland prairies that carpeted this landscape in 1830. It is our hope that not only will the existing plants and smaller animals find a larger, more stable home here, but also that larger species requiring more elbow room, such as short-eared owls, marsh hawks, and badgers, will be attracted to this 1,000-acre prairie. Combined with the adjacent 608 ha (1,500 acre) of Glacial Park being restored to prairie, savanna, and wetland, the 1,013-ha (2,500-acre) natural landscape may even support a small managed herd of introduced bison—"belly deep in a tall-grass sea."

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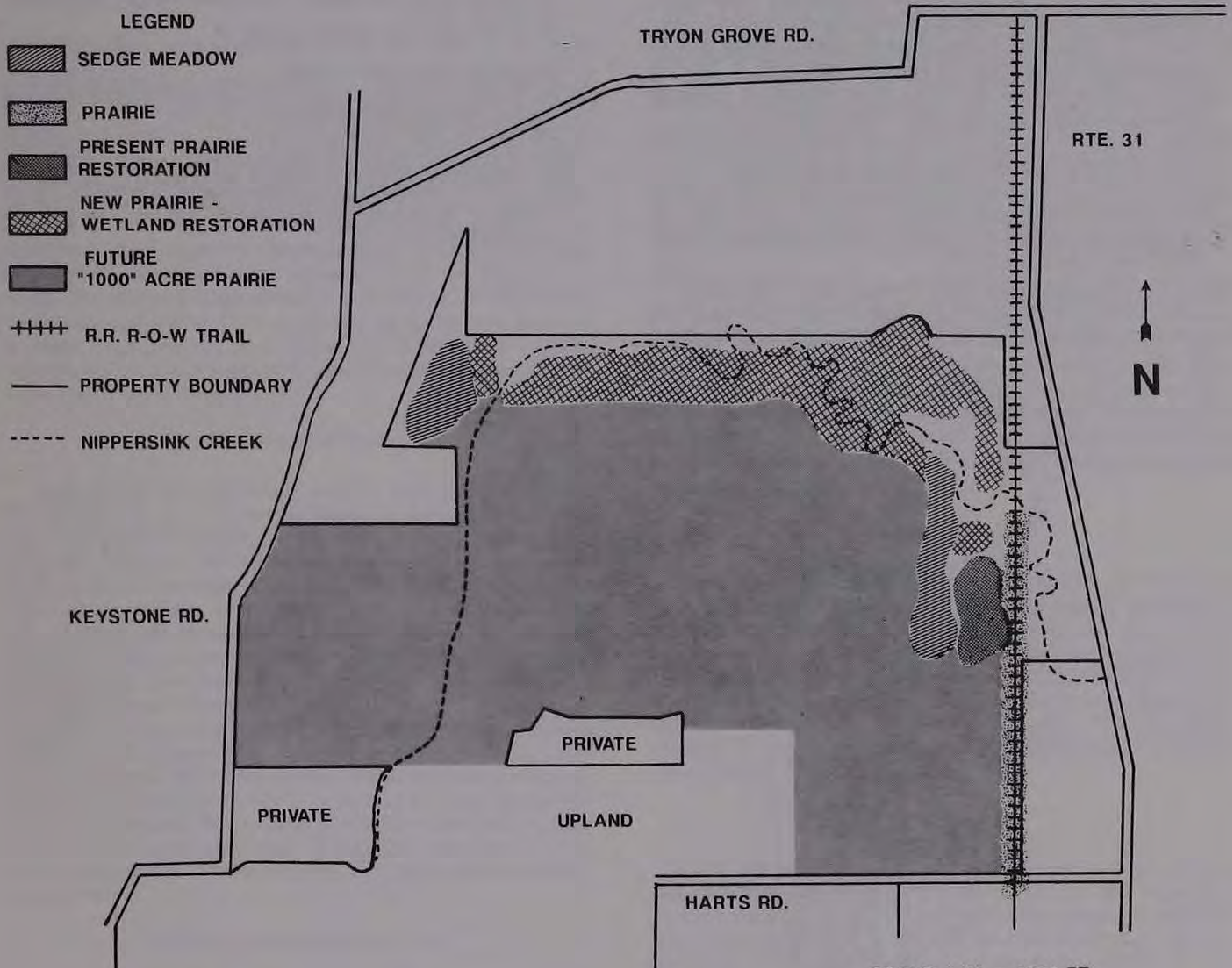

Figure 2. Glacial Park Management Plan Map.

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LEAFY SPURGE: THREAT TO CENTRAL PLAINS GRASSLANDS

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Abstract. Leafy spurge (*Euphorbia esula* L.) is a noxious weed that threatens grasslands in the central and northern Great Plains and the prairie provinces of Canada. Leafy spurge threatens prairie communities by displacing native species and reducing species diversity. Effective management of this undesirable plant requires that one be able to identify leafy spurge, understand the characteristics that contribute to its aggressive habit, and be aware of practices that are available to control this noxious weed. The aggressive habit of leafy spurge is related to its ability to reproduce both by seed and by numerous adventitious shoot buds located along an extensive root system. Effective seed dispersal mechanisms, high seed viability, and rapid seedling development enable new infestations to become established easily. Prolific vegetative reproduction maintains dense, long-lived infestations. Preventing the movement of leafy spurge propagules onto non-infested sites is the most effective method of reducing the spread of this non-endemic plant. Herbicides currently provide the most effective means to manage existing leafy spurge infestations.

INTRODUCTION

Leafy spurge (*Euphorbia esula* L.) is a serious noxious weed problem in the central and northern Great Plains and the prairie provinces of Canada (Watson 1985). The threat it poses to prairie preservation and restoration is primarily one of displacing native species and reducing plant diversity in native prairie communities. To reduce this potential loss of native plant species in prairie communities, it is essential to be able to identify leafy spurge, understand the characteristics that contribute to its aggressive habit, and be aware of practices that are available to control this noxious weed. The objective of this review is to provide information about the biology, ecology, and control of leafy spurge so those involved in prairie restoration and preservation will be better able to minimize the impact of this undesirable plant on native grasslands within the central Great Plains.

IDENTIFICATION

Leafy spurge stems are woody, hairless, erect, pale green, 30 to 100 cm tall, and occur in clumps (Figure 1). Leaves are alternate, narrowly linear with smooth margins, about 0.5 cm wide, 3 to 5 cm long, and glabrous. Flowering axillary branches are common. Seed are round to oblong, smooth, gray with a dark line on one side, and about 5 mm long (Wicks and Derschied 1964) (Figure 2A). Flowers are inconspicuous, greenish yellow, and occur in numerous small clusters with each cluster subtended by a pair of large yellowish heart-shaped leaves (bracts) arranged in a conspicuous umbel (Figure 1C and D). Flowers are borne in a cup-shaped cyathium containing one pistillate and 11 to 20 staminate flowers (Watson 1985) (Figure 2B). The margin of the cyathium bears four, two-horned nectiferous glands. Fruits are three-lobed capsules with one seed in each lobe (Figure 2C). A salient characteristic of leafy spurge is the presence of a milky white juice or latex that occurs throughout the plant (Hanson and Rudd 1933). The canary yellow bracts coupled with the white milky sap make identification easy.

ORIGIN AND INTRODUCTION

Leafy spurge is native to Eurasia. The first documented occurrence of leafy spurge in North America was in Newbury, Massachusetts in 1827 (Britton 1921). It is speculated that the arrival of leafy spurge along the eastern seaboard was facilitated by movement of propagules, seed or vegetative portions, in ballast deposited by ships originating from Europe (Dunn 1985). European ships would bring manufactured goods to the colonies and would return to Europe filled with raw materials. Because the manufactured goods were relatively lightweight, it was necessary for the ships to take on extra weight (ballast) in the form of soil to maintain stability while underway. Once the ships arrived in the colonies, the ballast was dumped on shore in preparation for loading raw materials for the return voyage.

Investigators proposed that the presence of leafy spurge in north-central North America resulted from migration of the weed from the eastern seaboard. However, this is unlikely because few plants occur in the intervening Great Lakes States (Dunn 1985). Other mechanisms appear responsible for the introduction of this weed into the north-central region of North America.

Crop seed imported from Russia and Europe was probably contaminated with leafy spurge seed and served as a means of introduction into north-central North America (Dunn 1985). Wheat (*Triticum aestivum* L). and oat (*Avena sativa* L.) seed were brought by Mennonites when they migrated from Russia during the 1870s and could have been contaminated with leafy spurge seed (Hanson and Rudd 1933). Early records of leafy spurge infestations in areas settle by the Mennonites support this means of introduction (Dunn 1985).

In the 1890s, cereal explorers with the United States Department of Agriculture (USDA) Bureau of Plant Introduction sent several different kinds of seed grain from Russia to the northcentral United States (Dunn 1985). Large quantities of smooth bromegrass (*Bromus inermis* L.) seed were imported from northern Europe and Russia for distribution in the northern United States. Contamination with leafy spurge and other exotic weeds was likely because of the rudimentary methods available for separating weed seed from crop seed during the late nineteenth century.

DISTRIBUTION

Leafy spurge is currently found in six provinces of Canada and 26 states in the United States. In 1979, the extent of infestation in North America was estimated at 1.0 million hectares (Dunn 1979). Despite early introduction into Massachusetts, leafy spurge is currently not a problem weed in the northeastern United States or eastern Canadian provinces. Presently, leafy spurge is a serious problem in North Dakota, South Dakota, Minnesota, Colorado, Idaho, Montana, Wyoming, Nebraska, and the prairie provinces of Canada (Dunn 1985).

PHENOLOGY

Leafy spurge shoot emergence begins in early March in Iowa and Nebraska (Bakke 1936). Stem elongation and vegetative development increase rapidly as temperatures increase in April and May. Shoots increase in number until early summer. Yellow bracts that subtend the flowers are visible from mid-May to mid-June and most conspicuous during peak flowering. Flowering of the terminal inflorescence ceases between the end of June and early

July. Seed maturation continues for 30 days after appearance of the last flower (Selleck et al. 1962). Thus, flower production and seed development is continuous from late May through August. Flowering and seed development can be renewed in the fall, and viable seed may be produced if growing conditions are favorable.

MORPHOLOGY AND BIOLOGY

The aggressive nature of leafy spurge is related to its phenomenal ability to reproduce prolifically both by seed and by numerous adventitious shoot buds located along an extensive root system. Effective seed dispersal mechanisms, high seed viability, and rapid seedling development enable new infestations to become established easily. Prolific vegetative reproduction maintains dense, long-lived infestations.

Seed and Seedlings

The leafy spurge fruit is a three-lobed capsule or schizocarp that splits into three, one-seeded nutlets (Porter 1967). Seed yields can range from 27 to 3800 kg/ha, depending on level of interference from associated plants and inherent site productivity (Selleck et al. 1962). Each flowering stem can produce up to 250 seed. Once seed are dispersed, they can remain viable for five to eight years (Selleck et al. 1962; Bowes and Thomas 1978). Leafy spurge seed germination in the field can occur throughout the growing season when moisture is adequate. Typically, early spring is the most favorable time for seed germination. Optimum seed germination occurs when temperatures fluctuate between 20 and 30 C (Selleck et al. 1962).

Leafy spurge seedlings can emerge through several centimeters of soil with optimum depth ranging from 1 to 5 cm (Selleck et al. 1962). Within 48 hr after emergence, the seedcoat is sloughed and cotyledons are exposed and begin to function like true leaves. Seedling roots can extend to 60 cm and stems can reach a height of 15 cm within 60 days after the cotyledons expand (Selleck et al. 1962). Vegetative buds develop on seedlings just above the soil surface 10 to 12 days after emergence or by the six-leaf growth stage. New shoots will arise from these buds once seedlings reach the 10-leaf stage if the seminal shoot is removed. Thus, leafy spurge makes the transition from seedling to perennial soon after germination. In the presence of competition, seedlings rarely produce flowers the first year. In disturbed areas, free from competing vegetation, Morrow (1979) reported that leafy spurge seedlings flowered the first year of growth.

Seed Dispersal Mechanisms

Leafy spurge seed are spread several ways. Seed are forcibly disseminated from individual plants as the capsule containing the seed dries. Sufficient force can be generated as the drying capsule shrinks and splits to throw a seed as far as 4.6 m (Hanson and Rudd 1933). Seed of leafy spurge can float on water and can germinate while floating (Bakke 1936). This ability enhances leafy spurge establishment in areas that flood periodically, such as ditches, streams, and river banks.

Birds and mammals act as seed dispersal agents (Hanson and Rudd 1933). Sharptail grouse (*Tympanuchus phasianellus*) and mourning dove (*Zenaida macroura*) consume large amounts of seed (Selleck et al. 1962). Viable seed have been found in droppings of sharptail grouse, but not in those of dove. However, dispersal by dove may be facilitated as seed are regurgitated when nestlings are fed (Blockenstein et al. 1987). Mammals may carry seed in mud on their feet or fur, and ingested seed may remain viable as they pass through an animal digestive tract.

Man has played a major role in leafy spurge seed dispersal. Seed has been widely dispersed as a contaminant in crop seed, feed grain, and hay. Leafy spurge has been found in oats, smooth brome, and alfalfa (*Medicago sativa* L.) seed. If not properly cleaned before leaving an infested site, contaminated tillage and harvest machinery can distribute seed or plant fragments.

Buds and Shoots

Two types of buds are present on leafy spurge. Axillary buds occur along aerial shoots and contribute to branching; adventitious buds arise below ground on roots and crowns (Figure 2D and E). Adventitious buds can be categorized as either reparative buds, produced following injury, or additional buds, produced spontaneously without any apparent injury (Raju et al. 1966). In established infestations, most shoots arise from adventitious buds along the crowns and not from the roots. Quiescence of leafy spurge root buds is caused by the presence of high concentrations of indole acetic acid (IAA) (Nissen and Foley 1987). When shoots are removed or the crown is damaged, endogenous concentrations of IAA decrease and root buds become active.

Roots

The root system of leafy spurge is composed of the main axis, or long roots, and laterals, or short roots (Raju et al. 1963). Long roots constitute the permanent root framework and have the capacity to regenerate roots and shoots. New vertical roots arise on the old roots, allowing root penetration to great depths. Individual long roots may live for up to four years in the field and may reach 5 m in length. Short roots do not persist or produce buds and are not considered part of the permanent root framework.

Regeneration of stems from buds on crowns and roots and limited translocation of herbicides to these perennating organs contribute to the resistance of this species to control (Lym and Moxness 1989). Although the upper portion of the plant can be killed by herbicides or tillage, the buds located below the treated zone can continue to produce new shoots. For example, Selleck et al. (1962) reported that leafy spurge stem density increased two-fold (113 to 265 shoots/m^2) following roto-tilling. Reserves in the roots provide the energy needed by the developing shoots before they emerge from the soil and become photosynthetically active. In Canada, leafy spurge shoots emerged within 113 and 365 days following burial of root fragments beneath 30 to 60 cm of weed free soil, respectively (Coupland et al. 1955).

WEED MANAGEMENT METHODS

There are three approaches to weed management: 1) prevention, 2) eradication, and 3) control (Klingman and Ashton 1975). Prevention is the process by which a weed species is not allowed to become established in a given area. Weed seed are not carried onto the area and existing weeds are not allowed to reproduce. Eradication is the complete elimination of all plants and seed from an area. Control limits the extent of infestation and enhances the competitive ability of desirable plants. Of these three approaches, prevention is the most cost effective.

Figure 1. Illustration of selected leafy spurge phenological stages; (A) dormant adventitious bud stage; (B) late vegetative stage with terminal leaves on main shoot axis enclosing floral bud; (C) flowering to early fruit stage with determinant inflorescence consisting of branched rays that are subtended by a whorl of bracts (note secondary inflorescence arising from axils of leaves on primary stem); (D) flowering-late fruit stage with inflorescence arising from a late-flowering shoot [scale: 10 mm = 25 mm].

Figure 2. Selected leafy spurge plant portions; (A) cyathium containing one pistillate flower and several staminate flowers (scale: 6 mm = 1 mm); (B) cyathium with 3-lobed fruit (scale: 8 mm = 1 mm); (C) side and front view of seed (scale: 4 mm = 1 mm); (D) adventitious shoot buds located on roots [scale: actual size] and (E) crowns (scale: 1 mm = 0.5 mm).


A
B
C
D
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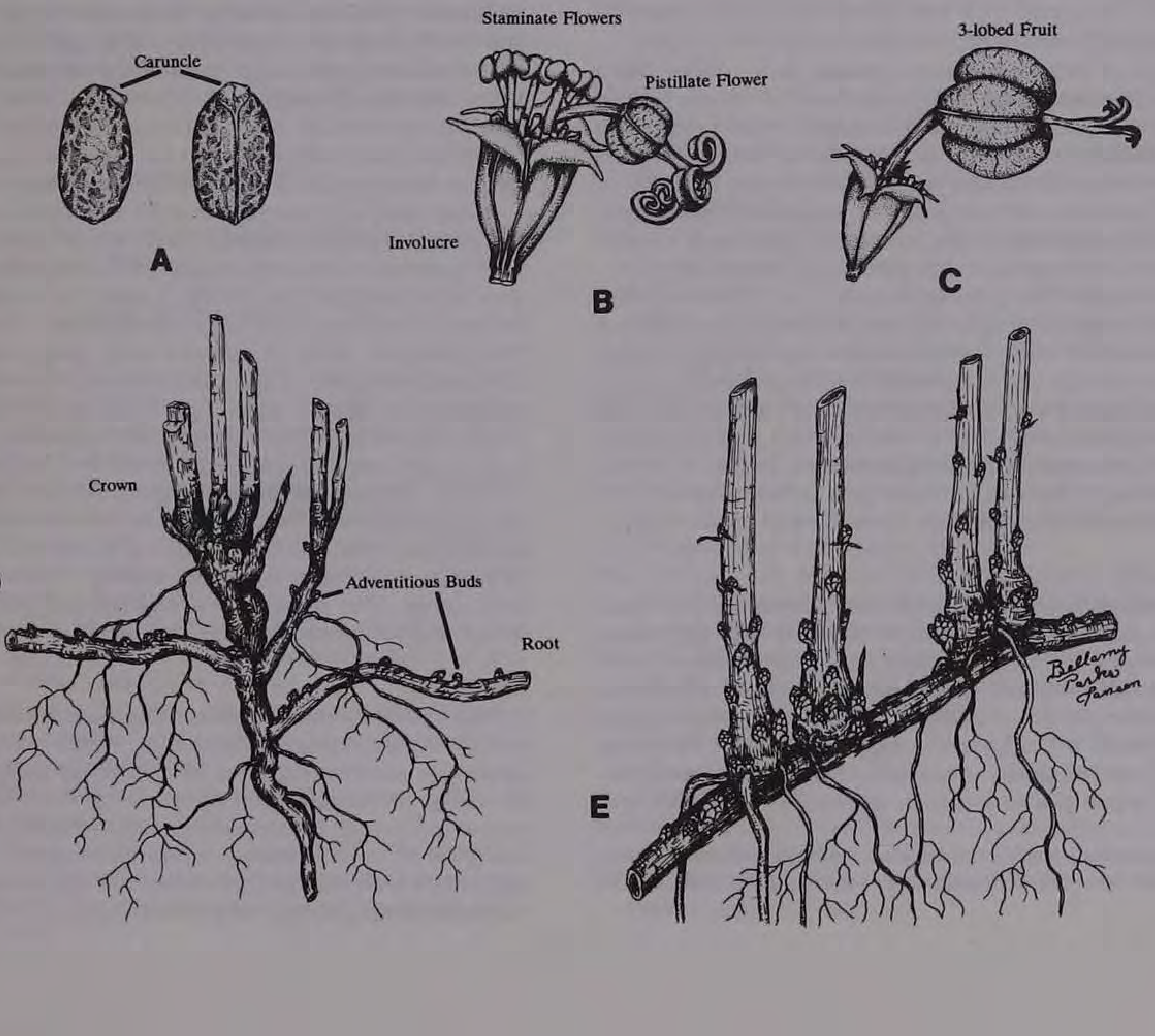
1


Caruncle
A
Staminate Flowers
Pistillate Flower
Involucre
B
3-lobed Fruit
C
Crown
D
Adventitious Buds
Root
E
Bellamy Parks Jansen

2

Limiting seed dispersal and maintaining a vigorous and stable prairie community will prohibit leafy spurge establishment (Best et al. 1980). Seed dissemination can be reduced during prairie restoration activities by planting native grass and forb seed that are free of weed seed and by cleaning farm machinery to ensure that it is devoid of leafy spurge seed before moving from infested to non-infested areas. Controlling leafy spurge seedlings with appropriate chemical treatments will slow the rate of leafy spurge encroachment (Alley and Messersmith 1985). Managing the prairie community in a manner that promotes the vigor of the native grasses and forbs will enhance their competitiveness with leafy spurge.

There are several methods used to manage weed populations. These methods include chemical, biological, mechanical, and fire treatments. The merits of these measures as they relate to leafy spurge control follow.

Chemical

The herbicides that are most frequently recommended to control leafy spurge are picloram [4-amino-3,5,6-trichloro-2-pyridinecarboxylic acid] (Tordon 22K), 2,4-D [(2,4-dichlorophenoxy)acetic acid], and glyphosate [N-(phosponomethyl)glycine] (Roundup)[1] (Lym and Messersmith 1985). What, how much, and when to use these herbicides depends on the size and location of the leafy spurge infestation and land manager objectives.

Small infestations.

Complete control of leafy spurge in small infestations (less than 100 m^2/ha) can be achieved by using picloram. Areas containing the small infestations should be monitored periodically (at least three times a year) and any leafy spurge regrowth treated before it becomes sexually reproductive. Picloram can be applied at a rate of 2.2 kg active ingredient (a.i.)/ha to top-kill leafy spurge (Lym and Messersmith 1985). For best results, the herbicide should be applied to the established stand and a 5 m wide strip around the perimeter of the infested area.

Large infestations.

Eradication of large infestations (greater than 1 ha) of leafy spurge is not economically or ecologically feasible. Generally, herbicide costs and the damage to desirable forbs is great when attempts to eradicate leafy spurge are made on the scale of the plant community. Large infestations are most effectively managed to reduce seed production and movement of propagules from the primary area where established plants occur. The objective is containment, to confine leafy spurge within the existing infestation.

Application of 2,4-D + picloram at rates 1.1 + 0.28 kg a.i./ha or 2,4-D alone at a rate of 2.2 kg a.i./ha provides short-term control of leafy spurge and will reduce seed production significantly. Repeated annual (five to eight years) applications of a combination of 2,4-D and picloram have been found to decrease leafy spurge stem density (Lym and Messersmith 1987). The optimum time of application is in the late spring, when the plants are at the late flowering phenological stage. Because leafy spurge is indeterminate, chemical treatments should be made when the most stems are flowering.

Tree understory.

Control of leafy spurge in the understory of trees is best accomplished with the amine formulation of 2,4-D or with glyphosate (Moomaw et al. 1989). Application of 1.1 kg a.i./ha of 2,4-D amine at late flowering will reduce seed production. Glyphosate applied at a rate of 0.84 kg a.i./ha in the fall before leafy spurge becomes dormant will suppress spurge regrowth the following growing season. Two points of caution: 1) glyphosate is nonselective and will injure grasses and forbs growing in association with leafy spurge, and 2) contact of tree foliage or green bark with either herbicide should be avoided.

Biological Control

In agricultural systems, the primary objective of biological control is not eradication, but rather use of natural enemies to lower the density of the target weed to non-economic levels (DeBach 1973). In prairie preserves, acceptable levels of leafy spurge reduction is determined by other than economic factors, including aesthetics and maintaining native plant diversity. Biological control agents include plant pathogens, insects, and livestock. The USDA-Animal Health and Plant Inspection Service and USDA-Agricultural Research Service are actively involved in identifying and collecting insects and pathogens from weeds in their native habitats. Confusion about the origin of leafy spurge in North America hinders the development of biocontrol programs. Leafy spurge in North America is not a single species but represents a complex of closely related, possibly hybridized, plants (Croziat 1945; Ratcliff-Smith 1985). As a result of this hybridization, the relationship between North American and Eurasian leafy spurge is unclear. Determination of this relationship will facilitate advances in biocontrol.

Despite confusion over the origin of leafy spurge, several insects have been approved for release in North America (Rees et al. 1990). These insects include the spurge hawkmoth (*Hyles euphorbiae*), root-boring beetles (*Apthona* sp.), the stem- and root-boring longhorn beetle (*Oberea erythrocephala*), and the gall-fly (*Spurgia esulae*). The spurge hawkmoth larvae feed voraciously on leafy spurge foliage but have not been successful in controlling leafy spurge because they are readily preyed upon by several types of insects (Forwood and McCarty 1980). The adult root-boring beetle deposits eggs in the stem of leafy spurge. As the larvae develop, they burrow through the center of the stem to the crown and root tissues. They feed on these tissues and disrupt the plant's ability to reproduce vegetatively. The stem- and root-boring longhorn beetle exhibits a feeding behavior similar to the root-boring beetle. These insects differ in that *Apthona* sp. are univoltine, and the *Oberea* is multivoltine. The eggs of the gall-fly are deposited on the terminal portions of the reproductive stems. The larvae that develop cause a gall to form at the shoot apex and eliminate seed production by prohibiting flowering. Most of these insects have been released within the last seven years, and it is too early to determine how effectively they will control leafy spurge.

Leafy spurge is poisonous to cattle and horses, but not to sheep and goats. Once accustomed to leafy spurge, sheep will eat sufficient quantities to maintain weight gains comparable to gains on a grass diet (Landgraf et al. 1984). Lambs have a tendency to scour and may die if they graze large mature plants. Continuous intensive grazing by sheep will prevent leafy spurge vegetative spread and seed production. Eight years of intensive continuous grazing reduced leafy spurge stem densities 98% (Bowes and Thomas 1978). However, within two years after cessation of grazing, the leafy spurge started to reestablish shoots, which arose from crowns and roots. If sheep are used, grazing should commence early in the spring, and mature stands should be mowed before grazing to improve palatability. Sheep should not be allowed in a non-infested pasture within nine days after leaving a pasture infested with leafy spurge. This period of time is required to ensure that all leafy spurge seed have passed through their digestive tracts.

Mechanical

Mechanical treatments can be categorized according to the portion of the plant removed (Scifres et al. 1980). Top growth removal consists of severing the aerial portion of the plant by mowing or shredding. In contrast, entire plant removal involves removing top-growth and enough of the below-ground portion of the plant to prevent plant regrowth. Mowing during flowering and before seed fill will reduce leafy spurge seed production (Derschied et al. 1985). Repeated mowing during the growing season for several years can

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[1] Mention of a pesticide in this paper does not constitute a recommendation by the USDA or University of Nebraska nor does it imply registration under FIFRA.

reduce leafy spurge stands by depleting plant energy reserves. However, the root system of leafy spurge is so extensive that energy reserve depletion is difficult to achieve. Entire plant removal techniques can be effective in a cropland environment where various tillage practices can be applied (Derschied et al. 1985). On prairies, such practices would have limited applicability.

Fire

Grasslands are fire-dependent ecosystems that are comprised of plants that not only tolerate fire, but require fire to promote growth and survival (Wright and Bailey 1982). Plant response to fire is dependent on several factors, including plant morphology, plant phenology, and season of burning. With creeping perennial herbaceous plants, like leafy spurge, fire alone is usually no more effective than a mowing treatment (Scifres 1980). However, there may be an opportunity to reduce the competitiveness of leafy spurge by burning late in the spring. In the late spring, leafy spurge is in the late vegetative to early flowering phenological stage while the native, perennial, warm-season grasses are initiating growth.

SUMMARY

Leafy spurge threatens the integrity of native grasslands in the central Great Plains. This adventive, creeping, herbaceous perennial possesses several characteristics that enable it to compete with and displace native prairie plants. As a result of its aggressive nature, leafy spurge must be controlled whenever it occurs near or in a native prairie community. Prevention of propagule movement onto non-infested sites is the most effective method of reducing the spread of this non-endemic plant. Herbicides currently provide the most effective means to manage leafy spurge infestations, despite promising advances in the search for biological control organisms and because it is resistent to fire and mechanical control. Managers responsible for the maintenance of native plant diversity in prairie communities must be vigilant and closely monitor these natural areas because early detection of leafy spurge invasion is essential to complete control. Once found, leafy spurge should be controlled before it can produce seed. Maintaining records of the location of infestations and conducting frequent surveys will help ensure that sites do not become reinfested.

ACKNOWLEDGEMENTS

Illustrations are by Bellamy Parks-Jansen, 2056 West and 300 South, Kokomo, Indiana 46902.

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EFFECTS OF FIRE AND ATRAZINE ON PASTURE AND REMNANT PRAIRIE PLANT SPECIES IN SOUTHERN IOWA

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Abstract. We used a 2 x 2 factorial design to evaluate the effects and potential interaction of fire and atrazine on the abundance of various plant species, including native prairie species, on southern Iowa pastures. Analyses of covariance showed that most cool-season perennial grasses were greatly decreased by atrazine but decreased significantly after fire only during a drought year. Warm-season annual grasses exhibited highly significant increases on atrazine plots, establishing in the habitat resulting from the elimination of cool-season grasses. Remnant populations of native prairie grasses were observed on some pastures; they exhibited less definitive responses although increases on atrazine plots did occur. Annual forb species tended to increase on fire plots. Atrazine significantly decreased several annual forbs but only during the year of treatment. A few native perennial forbs evaluated were not affected by either fire or atrazine. Significant fire by atrazine interactions were caused by three processes: 1) from atrazine negating any positive effects from fire, 2) from the presence of litter apparently interacting with atrazine, or 3) from a positive synergism whereby litter removal (by fire) and creation of open habitat (by atrazine) were required to achieve an effect.

INTRODUCTION

Since 1984, we have searched for remnant native prairie grasses on pastureland in southern Iowa and tried to determine if these remnants could be the basis for development of warm-season pastures. Because warm-season, native, perennial grasses (typically characterized by C4 photosynthesis) are highly productive during the hot summer months, they are a desirable component in the management of pasture forage for livestock production (Conard and Clanton 1963, Jung et al. 1978, Krueger and Curtis 1979, Hall et al. 1982). Grazing studies in Nebraska (Conard and Clanton 1963), Iowa (Wedin and Fruehling 1978), Pennsylvania (Jung et al. 1978), South Dakota (Krueger and Green 1976), and Missouri (Rountree et al. 1974) have demonstrated that incorporating a warm-season rotation into the grazing period can enhance the average daily weight gain of animals.

Pastureland in southern Iowa is typically dominated by exotic, cool-season grasses such as Kentucky bluegrass (*Poa pratensis* L.), redtop (*Agrostis alba* L.), smooth brome (*Bromus inermis* Leyss.), tall fescue (*Festuca arundinacea* Schreb.), timothy (*Phleum pratense* L.), and orchard grass (*Dactylis glomerata* L.). An experiment was designed to test the effectiveness of spring fire and atrazine treatments in eliminating or suppressing these cool-season grasses, while either enhancing or having a neutral effect on remnant populations of desired warm-season native grasses, specifically big bluestem (*Andropogon gerardi* Vitman), Indian grass (*Sorghastrum nutans* (L.) Nash), little bluestem (*A. scoparius* Michx.), and side-oats grama (*Bouteloua curtipendula* (Michx.) Torr.).

The positive effects of spring fire on the growth of warm-season grasses in tallgrass prairie habitat are well documented (reviewed by Glenn-Lewin et al. 1990, and Rosburg 1990). The removal of accumulated litter by fire immediately prior to the initiation of warm-season growth fosters higher photosynthetic rates and productivity, probably because of a more favorable temperature and light environment and more favorable nitrogen dynamics (Hulbert 1969, Old 1969, Peet et al. 1975, Rice and Parenti 1978, Knapp 1984, Knapp and Seastedt 1986). Because cool-season growth begins several weeks prior to that of the warm-season species, perennial cool-season grasses can incur considerable physiological stress when a fire consumes or kills their above-ground biomass. Decreases in cool-season productivity or cover after a spring fire have been reported in South Dakota (Engle and Bultsma 1984, Gartner et al. 1986), Montana (White and Currie 1983, Antos et al. 1983), Illinois (Old 1969), Nebraska (Hover and Bragg 1981, Nagel 1983, Schacht and Stubbendieck 1985), Minnesota (Svedarsky and Buckley 1975), Wisconsin (Diboll 1986), Iowa (Hill and Platt 1974, Rosburg 1990), and Alberta (Anderson and Bailey 1980).

Atrazine [2-chloro-4-(ethylamino)-6-(isopropylamino)-s-triazine] is a selective herbicide widely used for control of broadleaf and grassy weeds in many crops. It is primarily absorbed through the roots and translocated to apical meristems and leaves, where it inhibits photosynthesis by interfering with CO_2 fixation in the Hill reaction (Van Assche and Ebert 1976). The suitability of atrazine in the restoration of remnant native grasses hinges on its selectivity. Perennial, warm-season, native grasses generally have exhibited tolerance to normal rates of atrazine application, while some cool-season grasses and annual plant species have shown susceptibility (Brejda et al. 1989, Rice and Stritzke 1989, Dill et al. 1986, Petersen et al. 1983, Waller and Schmidt 1983, Martin et al. 1982, and Houston 1977). Atrazine tolerance occurs in plants with the physiological ability to metabolize and degrade atrazine or in deep-rooted perennials that uptake minimal amounts of atrazine (Herbicide Handbook Committee 1983). Tolerance may also occur in some species because chloroplast mutation has altered the site of atrazine attachment in electron transport (Salisbury and Ross 1985).

Our research goals included 1) assessment of the occurrence of remnant prairie species, primarily perennial grasses, on southern Iowa pastureland and 2) evaluation of the effects of spring fire and atrazine treatments, and their potential interaction, on pasture and remnant prairie plant species.

METHODS

Experimental treatments were applied to stands of pastureland in Ringgold, Union, and Decatur counties in south-central Iowa, within the Southern Iowa Drift Plain (Prior 1976). The climate is temperate and continental. Annual precipitation averages 77 to 80 cm, most of which falls during the spring and summer. Average minimum and maximum daily January temperatures are -11 C and 0 C, respectively; corresponding daily July temperatures are 18 C and 31 C, respectively. The average growing season is 165 days.

Livestock exclosures (the statistical equivalent of blocks) were constructed from cattle panels so that they contained four plots, each 2.44 m by 2.44 m. The exclosures were located to minimize variation in slope, aspect, and soil type. A factorial arrangement of fire and atrazine, each either present or absent, resulted in four treatments: control (albeit a release from grazing), fire, atrazine, and fire plus atrazine. A randomized block design was used to distribute these four treatments in each exclosure (block). A total of thirty-six replications of the four treatments were monitored on 11 pastures.

Exclosures were erected in 1984; a baseline inventory of all plots was conducted in 1985; and treatments were applied and plot inventories were completed in 1986, 1987, and 1988. Inventories in 1985 and 1986 were accomplished by measuring the relative shoot frequency (RSF) of species with a 10-pin sampling frame

Table 1. Explanation of experimental structure.

Response measured	*Experimental[a] COV/RES*	*Treatment date*	*Pasture group*	*Replicates*	*Response measurement[b]*
The same year as treatment	85/86	March 86	A	21	RSF
	86/87	April 87	B	14	BIO
	87/88	April 88	A	16	BIO
One year after treatment	85/87	March 86	A	18	BIO
	86/88	April 87	B	14	BIO
Following a double treatment	85/88	March 86 April 88	A	16	BIO

[a] Experiment identifies a unique combination of pretreatment and response data. COV indicates inventory that provides the covariate, and RES the inventory that provides the response variable.

[b] RSF = relative shoot frequency, BIO = biomass measurements.

systematically placed 20 times in each plot, for a total of 200 hits. In order to obtain absolute data, inventories in 1987 and 1988 were performed by measuring biomass (BIO) from five stratified random subsamples (total area 0.5 m²) on each plot. The current year's peak standing biomass was cut at ground level, sorted by species, oven dried at 65 C, and weighed to the nearest 0.1 gram.

Fires were confined to burn plots by placing concrete wall boards vertically along the plot borders and wetting the perimeter with water. Backfires were used to burn the plots. Any unburned patches were re-ignited to obtain a burn result as homogeneous as possible. Fire was applied between March 23 and 28 in 1986, on April 11 and 12 in 1987, and between April 13 and 20 in 1988.

Approximately 7 to 10 days after the burning treatment, atrazine was applied with a hand sprayer at the rate of 2.2 kg of active ingredient per ha. Concrete boards were placed flat on the ground over adjacent plots to prevent accidental drift. Approximately 3.75 l water were used as the carrier per treated plot. No evidence of lateral movement in the soil by the atrazine was observed, although heavy rainfall after atrazine application on the Crittenden pasture in 1986 caused atrazine to leach downhill out of the exclosures.

When treatments began in 1986, the 11 pastures were divided into two groups (Table 1). One group (A) was initially treated in 1986, the other group (B) was initially treated in 1987. In 1988, the first group (A) was treated in the same manner as in 1986. Six different experiments were analyzed by considering all possible combinations of comparisons between the initial species composition of plots and their post-treatment composition (Table 1).

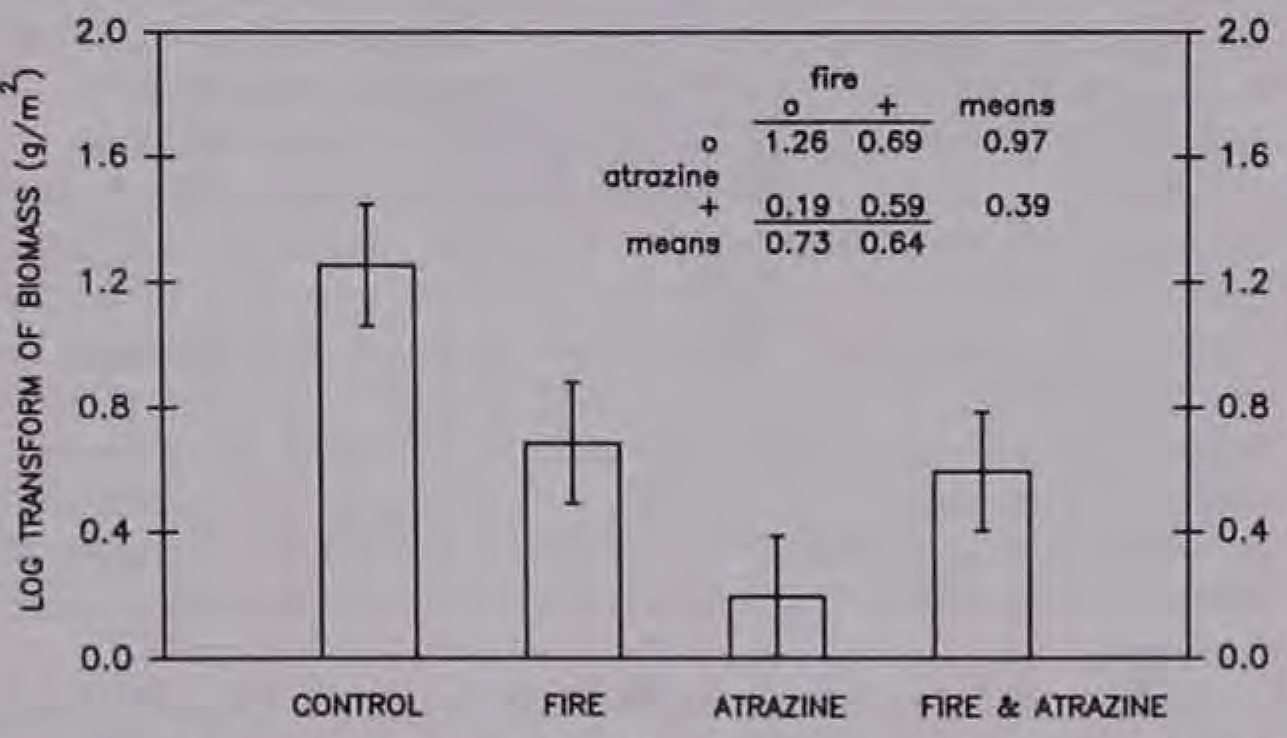

Figure 1. An example of the Least Squares means (with one standard error) and the main effects derived from the ANOCOV for each species. This example shows smooth brome for experiment 85/88.

In order to ascertain the effects of the treatments on plant species, it was important to account for the initial variation in the abundance of a species among the plots. For this reason, Analysis of Covariance (ANOCOV) was used to test for treatment effects. The abundance of a species in a plot the year before treatment was the covariate, and the abundance after treatment was the response. Although it has not been commonly used in fire research, ANOCOV is a useful technique for dealing with the natural heterogeneity that occurs in vegetation.

Two additional problems were solved by using ANOCOV. It allowed us to evaluate the 1987 treatments (measured by biomass) using the 1986 pretreatment data (measured by relative shoot frequency) as a baseline. Also, because the 1988 treatments were applied to plots that were treated initially in 1986, they had considerable potential for large differences in species composition prior to the 1988 treatments.

Tests of normality indicated that neither measure of species abundance, RSF nor BIO, was normally distributed. Therefore, all data were transformed so that they conformed more adequately to the assumptions of ANOCOV. As the data approach normality, they also become more homoscedastic (equal variances), and this insures additivity of the treatment effects (Sokal and Rohlf 1981). The relative shoot data were transformed as the arcsine of the square root of the proportion of a species, that is,

$$\text{arcsine } \sqrt{\text{RSF}/100}.$$

Biomass data were transformed as $[\log10\ (Y + 1)]$, where Y is the biomass measurement in g/m². A more detailed account of the methods is available in Rosburg (1990).

Data were subjected to Analysis of Covariance using the Statistical Analysis System PROC GLM (SAS Institute Inc. 1985). Analyses were performed on 40 taxa; including 28 grass and 12 non-grass taxa. An example of an ANOCOV table (Table 2) and an illustration of the corresponding Least Squares means (Figure 1) is presented for smooth brome in the 85/88 experiment. These results, as well as figures that illustrate the species' post-treatment abundance in a non-transformed scale, are presented for all taxa in Rosburg (1990).

Table 2. An Analysis of Covariance table was obtained for all species. This example shows the smooth brome response for experiment 85/88.

Source	*Degrees of freedom*	*Mean square*	*F value*	*Prob > F*
Covariate	1	0.0509	0.46	0.527
Pastures	2	0.1443	1.31	0.349
Treatments	3			
(fire)	1	0.0209	0.19	0.681
(atrazine)	1	0.9899	8.97	0.030
(fire*atrazine)	1	0.6924	6.28	0.054
Error	5			
Total	11			

RESULTS AND DISCUSSION

At least 137 plant taxa were encountered in the plot inventories over the four-year period of the project (see Rosburg 1990 for a complete list). Nomenclature for the grasses follows Pohl (1966), while Steyermark (1963) was used for other species, and grasses not in Pohl.

Remnant populations of native prairie grasses were observed on 7 of the 11 pastures. Big bluestem (on four pastures), little bluestem (on two pastures), and sideoats grama (on two pastures) occurred in treatment plots and were analyzed as a group labeled C4 forage grasses. Although Indian grass did not occur on any of the treatment plots, it was observed adjacent to the exclosures on three pastures. Tall dropseed (*Sporobolus asper* (Michx.) Kunth.) was the most common native grass, occurring on six pastures. Eastern gama grass (*Tripsacum dactyloides* L.) was present on one pasture.

Native prairie forbs observed either on treatment plots or in the pasture adjacent to exclosures included butterfly milkweed (*Asclepias tuberosa* L.), compass plant (*Silphium laciniatum* L.), rosinweed (*S. integrifolium* Michx.), blue-eyed grass (*Sisyrinchium campestre* Bickn.), prairie wild indigo (*Baptisia leucophaea* Nutt.), white wild indigo (*B. leucantha* T.& G.), many-flowered scurf pea (*Psoralea tenuiflora* Pursh), tuberous Indian plantain (*Cacalia tuberosa* Nutt.), and bush-headed clover (*Lespedeza capitata* Michx.).

Atrazine was the most effective treatment factor for suppressing cool-season grasses (Table 3). Substantial decreases in Kentucky bluegrass, Canada bluegrass (*Poa compressa* L.), and redtop were still evident one year after atrazine application. Similar decreases in *Poa* spp. after atrazine treatment have been observed in Nebraska (Waller and Schmidt 1983, Dill et al. 1986, Brejda et al. 1989).

Smooth brome was not as susceptible to atrazine as bluegrass and redtop although a significant reduction occurred during the 1988 treatment, which might have been due to an interaction with the severe drought of that year. Waller and Schmidt (1983) and Dill et al. (1986) also reported that smooth brome was at least moderately tolerant of atrazine. The only cool-season grass that did not exhibit any susceptibility to atrazine was tall fescue. Atrazine also

Table 3. Effect of fire (F), atrazine (A), and fire plus atrazine (X) treatments on selected plant species when compared with the control.

	85/86			*85/87*			*86/87*			*86/88*			*87/88*			*85/88*		
Species	*F*	*A*	*X*	*F*	*A*	*X*	*F*	*A*	*X*	*F*	*A*	*X*	*F*	*A*	*X*	*F*	*A*	*X*
K. bluegrass	ns	- - -	- - -	ns	- - -	- - -	ns	- -	- -	ns	ns	ns	- - -	- - -	- - -	- - -	- - -	- - -
redtop	ns	- - -	- - -	ns	- - -	- - -	ns	- -	- -	ns	ns	ns	ns	-	ns	ns	- - -	- - -
smooth brome	ns	ns	ns	ns	- -	- -	ns	ns	ns	ns	ns	ns	- -	- - -	- -	-	- -	-
tall fescue	+	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Canada bluegrass	ns	- - -	ns		NA		ns	ns	ns		NA		ns	ns	- -		NA	
C4 forage grass[a]	ns	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
tall dropseed	ns	ns	ns	ns	ns	ns	ns	+	++	ns	ns	ns	ns	ns	ns	ns	ns	ns
C4 weedy grass[b]	ns	ns	+		NA		ns	ns	ns		NA		ns	ns	ns		NA	
fall panicum	ns	+++	+++	ns	ns	++	ns	ns	+	ns	ns	ns	ns	ns	ns	ns	ns	+++
foxtail grasses	ns	++	++	ns	+	++	ns	++	++	ns	ns	ns	ns	ns	ns	ns	ns	ns
crabgrasses	ns	++	++	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	+	ns	+	ns
witchgrass		NA			NA		+++	-	-	ns	ns	ns		NA			NA	
panic grasses	ns	+++	+++	ns	++	+	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
prairie 3-awn	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Japanese brome		NA		ns	ns	ns		NA			NA		- -	-	- -	- - -	- -	- - -
sedges	ns	ns	+	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
common ragweed	ns	ns	ns	ns	ns	+++	ns	ns	- -	ns	ns	ns	ns	ns	ns	ns	-	-
fleabanes	ns	-	-	ns	ns	ns	ns	- -	- -	ns	ns	ns	ns	-	-	ns	- -	- -
asters	ns	-	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	- -	- -	ns	- -	- - -
ox-eye daisy	ns	ns	ns		NA			NA			NA		ns	ns	ns		NA	
wild carrot	ns	ns	ns		NA		ns	ns	ns		NA			NA			NA	
birdsfoot trefoil	ns	ns	ns		NA		ns	ns	ns		NA		ns	ns	ns		NA	
K. lespedeza	ns	ns	-		NA		ns	ns	-		NA		ns	ns	ns		NA	
sweet clover		NA			NA		ns	- -	- -		NA			NA			NA	
Baldwin ironweed	ns	ns	ns		NA			NA			NA		ns	ns	ns		NA	
rosinweed		NA			NA		ns	ns	ns		NA			NA			NA	
flowering spurge		NA			NA		ns	ns	ns		NA			NA			NA	

Notes: NA=Not Analyzed; ns=no significant effect; - or +, significant at P=0.1; - - or ++, significant at P=0.05; - - - or +++, significant at P=0.008. Minus signs (-) indicate a decrease; plus signs (+) indicate an increase.

[a] Includes big bluestem, little bluestem, and sideoats grama.

[b] Includes purple lovegrass (*Eragrostis spectabilis*), nimblewill (*Muhlenbergia schreberi*), fall witchgrass (*Leptoloma cognatum*), and paspalum (*Paspalum setaceum*).

suppressed several common weedy forbs, at least during the same year as treatment (Table 3).

The open habitat created by the elimination of cool-season grasses was colonized by warm-season annual grasses (Table 3). Except for 1988, very substantial increases in fall panicum (*Panicum dichotomiflorum* Michx.), foxtails (*Setaria* spp.), and crabgrasses (*Digitaria* spp.) occurred in each treatment year. These species' annual habit, combined with atrazine tolerance, made them ideally suited to the disturbance caused by atrazine. The absence of warm-season annuals in 1988 may be explained by inadequate moisture for seed germination during the drought conditions.

Treatments involving atrazine were the only ones that caused increases in perennial warm-season grasses. However, the increases were not as great as the decreases exhibited by cool-season species. The fire plus atrazine treatment appeared to be the most beneficial for tall dropseed, followed by atrazine alone. This observation, combined with the lack of a beneficial effect from fire, suggests that competition with cool-season grasses was more of a limiting factor on warm-season grasses than was litter accumulation.

Our study, which indicates that fire had very little effect in suppressing exotic cool-season grasses and enhancing warm-season prairie grasses, contradicts previous fire literature. There are several possible explanations for this discrepancy. First, the March burn date in 1986 probably was too early to have a negative impact on the cool-season grasses. Fire imparts the greatest physiological stress on a herbaceous perennial when it occurs during its period of optimum growth, by killing its current topgrowth and forcing regrowth from energy reserves in the roots. If the fire coincides closely with the initiation of cool-season growth, beneficial factors associated with litter removal could actually increase the abundance of cool-season species (Table 3, tall fescue and Canada bluegrass in 85/86).

Second, most of the research that reports increases in native, perennial, warm-season grasses due to fire has been done in prairielike habitat, where warm-season grasses are the major component and cool-season exotic grasses a minor component. When the heavy litter accumulations that can occur on prairies are burned off in late spring, the increase in abundance of native grasses comes from increased productivity. The exotic cool-season species not only suffer physiological stress from forced regrowth but also competitive stress from a more vigorous stand of warm-season grasses.

The situation in southern Iowa was essentially reversed. At the time the exclosures were erected, most pastures were badly overgrazed and had no litter accumulation. Because there were no inhibitory litter accumulations, any "release from litter" response would not be expected. Furthermore, the native prairie grasses were remnants in cool-season swards, and thus, the fuel load consisted of a higher proportion of green biomass. The relatively cooler fires might have resulted in less initial stress on the cool-season grasses. Also, the depauperate condition of remnant native plants suggests little if any competitive factor that would add to the stress on cool-season grasses.

Finally, fire could exert a positive benefit on the native grasses by opening up habitat for seedling recruitment from the seedbank. However, seedbank studies on these pasturelands indicate native prairie grasses are essentially absent from the seedbank (Akey 1989).

The species that did exhibit increases after fire were annuals: fall panicum, witchgrass (*Panicum capillare* L.), and common ragweed (*Ambrosia artemisiifolia* L.). Our observations support an assertion that fire in these pastures increases the abundance of annual species by opening up a temporary, sunny, exposed habitat favorable for their germination and establishment. That spring fires enhanced seedling establishment on prairies was noted by Curtis and Partch (1948) in Wisconsin, and by Johnson (1987) in central Iowa when growing season precipitation was above average.

Significant fire by atrazine interactions occurred in some instances. We observed three mechanisms by which a fire by atrazine interaction was generated. One was a situation in which the separate factors had opposite effects, and, when combined, one of the effects predominated rather than both "neutralizing" each other. An example is witchgrass (Table 3, 86/87), an annual grass. Fire alone enhanced its abundance, and atrazine alone reduced its abundance. When combined, atrazine prevailed by negating any increase generated by the fire 10 days earlier. This type of interaction might be predicted for annual species that are susceptible to atrazine.

Another situation occurred in which the separate factors had similar effects, but one was much more significant than the other. When combined, instead of being additive, the effect was similar to the least significant factor. An example of this situation is smooth brome (Table 2, Figure 1). When used alone, atrazine caused a more significant reduction than fire. When fire and atrazine were combined, the result was similar to the effect of fire alone. In this case, it appears that the litter that occurred on the atrazine plots was an important factor and probably interacted with the atrazine to decrease smooth brome.

The third case demonstrated a true, positive synergism, whereby both factors were required to achieve a response. An example of this situation was the response of common ragweed one year after treatment. Separately, fire and atrazine did not effect much response, but, on the fire plus atrazine plots, significant increases occurred (Table 3, 85/87). The removal of litter by fire and the creation of vacant habitat by atrazine were both necessary to achieve the large increase in common ragweed that was observed.

Plant species are summarized by same year fire effects in Table 4 and by same year atrazine effects in Table 5. In most cases, fire plus atrazine effected responses very similar to atrazine alone. Also, none of the native prairie forbs that occurred in atrazine plots exhibited any noticeable susceptibility to atrazine. Native grasses were tolerant of both spring fire and atrazine treatments, and some indications of positive responses occurred. On two pastures, productive stands of native prairie grasses were attained; their standing peak biomass ranged from 500 to 700 g/m^2. However, most of this restoration was due to the removal of grazing. The response of the remnant plants on the control plots to the removal from grazing was great enough that the fire or atrazine treatments could not effect a significantly higher response.

Table 4. Summary of same year effects of fire on plant species.

Increased	*Decreased*	*Unchanged*
tall fescue	Kentucky bluegrass	redtop
Canada bluegrass	smooth brome	big bluestem
witchgrass	rosette panic grasses	little bluestem
C4 annual grasses (as a group)[a]	Japanese brome	sideoats grama
	fleabanes	tall dropseed
		fall panicum
		yellow foxtail
		giant foxtail
		smooth crabgrass
		prairie three-awn
		sedges
		common ragweed
		asters
		ox-eye daisy
		wild carrot
		birdsfoot trefoil
		Korean lespedeza
		sweet clover
		Baldwin's ironweed
		rosinweed
		flowering spurge
		C4 perennial weedy grasses (as a group)[b]

[a] Includes fall panicum, foxtail species, and crabgrass species.

[b] Includes purple lovegrass, nimblewill, fall witchgrass, and paspalum

able 5. Summary of same year effects of atrazine on plant ecies.

creased	*Decreased*	*Unchanged*
ll dropseed	Kentucky bluegrass	big bluestem
ll panicum	redtop	little bluestem
llow foxtail	smooth brome	sideoats grama
ant foxtail	Canada bluegrass	tall fescue
nooth crabgrass	witchgrass	birdsfoot trefoil
sette panic grasses	Japanese brome	ox-eye daisy
dges	prairie three-awn	Baldwin's ironweed
4 perennial	asters	flowering spurge
weedy grasses	fleabanes	rosinweed
(as a group)	common ragweed	
	wild carrot	
	Korean lespedeza	
	sweet clover	

Intuitively this makes sense, because the pastures' histories of avy grazing pressure suggest that grazing was the most important ctor limiting the abundance of native prairie grasses. Neither fire, ich removes the inhibitory effects of litter accumulation, nor azine, which most effectively removes competition with cool-ason grasses, was initially as important as the removal of grazing. is possible that either fire or atrazine could increase the abun-nce of native grasses after their initial rebound. Our study does t indicate that to be true, but perhaps a longer study could plore this possibility.

Native prairie grasses and forbs exist on southern Iowa pastures, d they can be successfully recovered. However, whether grasses n be restored to the extent that they provide warm-season pas-age is a more complex question because the occurrence of rem-nt plants is the limiting factor. In a continously grazed pasture, visibility of remnant plants is very low; therefore, it is difficult estimate how much area remnant plants occupy. Our experience th 11 different pastures suggests that they occur in small patches, rhaps up to 1 ha in size, but more often much smaller. Given this her scattered occurrence of remnant plants to work with, it seems likely that a landowner could reclaim a warm-season pasture of fficient size. Alternatively, the remnant patches could be supple-nted by seeding native grasses into the sod. Acceptable stands intermediate wheatgrass (*Agropyron intermedium* (Host) Beauv.) d switchgrass (*Panicum virgatum* L.) resulted from sod-seeding periments in eastern Nebraska if adequate herbicide suppression the above-ground herbage was achieved (Samson and Moser 82).

Drought conditions caused reductions in productivity of about % to 50%, and likely interacted with fire to cause significant creases in Kentucky bluegrass and smooth brome, although a fire drought interaction cannot be conclusively established because effects are not separable in our design (a drought plot and a nor-l precipitation plot combined with the presence and absence of would be required). Because the only decreases of cool-season ennials after fire occurred in the drought year, there is a strong ggestion that an interaction was invloved. Furthermore, this ds us to suspect that the significance of interactions between fire d other "uncontrollable" factors (e.g., insect herbivory, competi-n) has been overlooked in much of the fire literature. In which e, claimed fire effects may in actuality be effects produced by interacting with other factors. Such interactions are just one of eral methodological problems in fire research (Glenn-Lewin et 1990). Numerous others, such as problems in experimental sign (e.g., what is a true control in a fire study?), the variability used by patch structure and growth form in vegetation, the vari-lity in fire characteristics, and problems in data analysis, add to difficulties of interpreting fire research.

ACKNOWLEDGMENTS

We thank the Soil Conservation Service and the Southern Iowa Agriculture Boosters for their financial support. Thanks to Dennis Hilger and Warren Angus for their help and support throughout the project and to Gerry Shimek and Robert Dahlgren for their help in initiating and organizing the project. Considerable assistance with the field work was provided by Ann Kosek Akey.

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MORPHOLOGICAL CHARACTERISTICS OF SMOOTH BROME USED TO DETERMINE A PRESCRIBED BURN DATE

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Abstract. The invasion and persistence of smooth brome (*Bromus inermis* Leyss.) is a serious problem facing managers of prairie remnants on the northern Great Plains and true prairie. Although several studies have demonstrated smooth brome is most easily damaged by grazing or cutting after tiller elongation begins, use of prescribed fire to control smooth brome has achieved only limited success. This study quantified changes in smooth brome tiller density following burning at three morphological growth stages. Burning smooth brome in mid-May, when tillers were elongating, and in late May, at tiller heading, reduced fall tiller density about 50% as compared to unburned control plots. Burning in early spring, when tillers were emerging, produced no reduction of fall tiller density. Unelongated and elongated tillers were characterized by leaf number and height. The number of green leaves per tiller is an easily observed indicator of smooth brome susceptibility to fire.

INTRODUCTION

Smooth brome (Bromus inermis Leyss.) is a cool-season, Eurasian grass introduced to the west coast of North America in the 1880s (Archer and Branch 1953). Smooth brome is widely planted as a drought-resistant forage and cover crop. It has a transcontinental range, as shown in Figure 1 (Stubbendieck et al. 1982).

A serious problem facing managers of many prairie remnants of the northern Great Plains and true prairie is the invasion and persistence of exotic cool-season grasses, particularly smooth brome. Smooth brome is a deeply rooting, rhizomatous perennial that often excludes other species, thus contributing to the reduction of native species diversity and biomass in natural areas.

Figure 1. Smooth brome (*Bromus inermis* Leyss.) distribution in North American.

Several studies (Reynolds and Smith 1962, Teel 1956, and Eastin et al. 1964) demonstrated that smooth brome is most easily damaged by grazing or cutting after tiller (shoot) elongation begins. Tiller elongation elevates the growing point of the plant above the ground surface. Lawrence and Ashfore (1964) indicated that elevation of the tiller growing point to more than 3 cm above the soil surface made the growing point susceptible to removal by grazing or cutting. Once the growing point is removed, regrowth can only take place by the initation of new tillers from basal buds (Figure 2). Paulsen and Smith (1968) found that smooth brome cut at this stage showed slow recovery because basal buds were poorly developed and root carbohydrate (energy) levels were low.

Use of prescribed fire to control or reduce smooth brome in degraded native prairie has achieved some success. Gates et al. (1982) found that burning overgrazed tallgrass prairie in eastern Nebraska in late April resulted in lower basal cover of smooth brome in the first year, but cover increased to original levels by the following year. Old (1969) showed smooth brome decreased in a warm-season prairie in Illinois with late April burning. She attributed this decrease to an advanced stage of development of smooth brome at the time of burning.

This study was initiated to quantify changes in smooth brome tiller density following burning at three distinct morphological growth stages: at tiller emergence, during tiller elongation, and at heading. Also, unelongated and elongated tillers were characterized by leaf number and height.

METHODS

The study was conducted at the University of Nebraska, Agricultural Research and Development Center, near Mead, Nebraska. The study area is part of a 8 ha planted field dominated by smooth brome and big bluestem (*Andropogon gerardii* Vitman).

In October 1988, the study area was divided into sixteen , 6 x 6m plots (36 m^2) surrounded by 1.5-m mowed lanes. The density of smooth brome tillers was determined for each plot by counting all current-year tillers in ten 0.1 m^2 randomly placed microplots. One of four treatments was applied to each 36 m^2 in spring 1989 in a complete randomized design with four replicates per treatment. Treatments included plots burned at tiller emergence (late March), at tiller elongation (mid-May), and at heading (late May) stages, and an unburned control. A back fire was used to burn each plot (Wright and Bailey 1982). The changes in smooth brome density were determined by resampling the plots in fall 1989.

An analysis of covariance (ANACOVA) coupled with a means comparison test (Duncan 1975) was used to determine tiller density differences among treatments. Fall 1988 tiller density was the covariate.

Control plots were used to characterize elongated and unelongated tillers. On 7 and 14 May 1989, ten randomly selected tillers (20 total) were classified as elongated or unelongated by examining for above-ground nodes. Each tiller was measured from the soil surface to the tip of the longest vertically stretched leaf, and the number of green leaves was recorded.

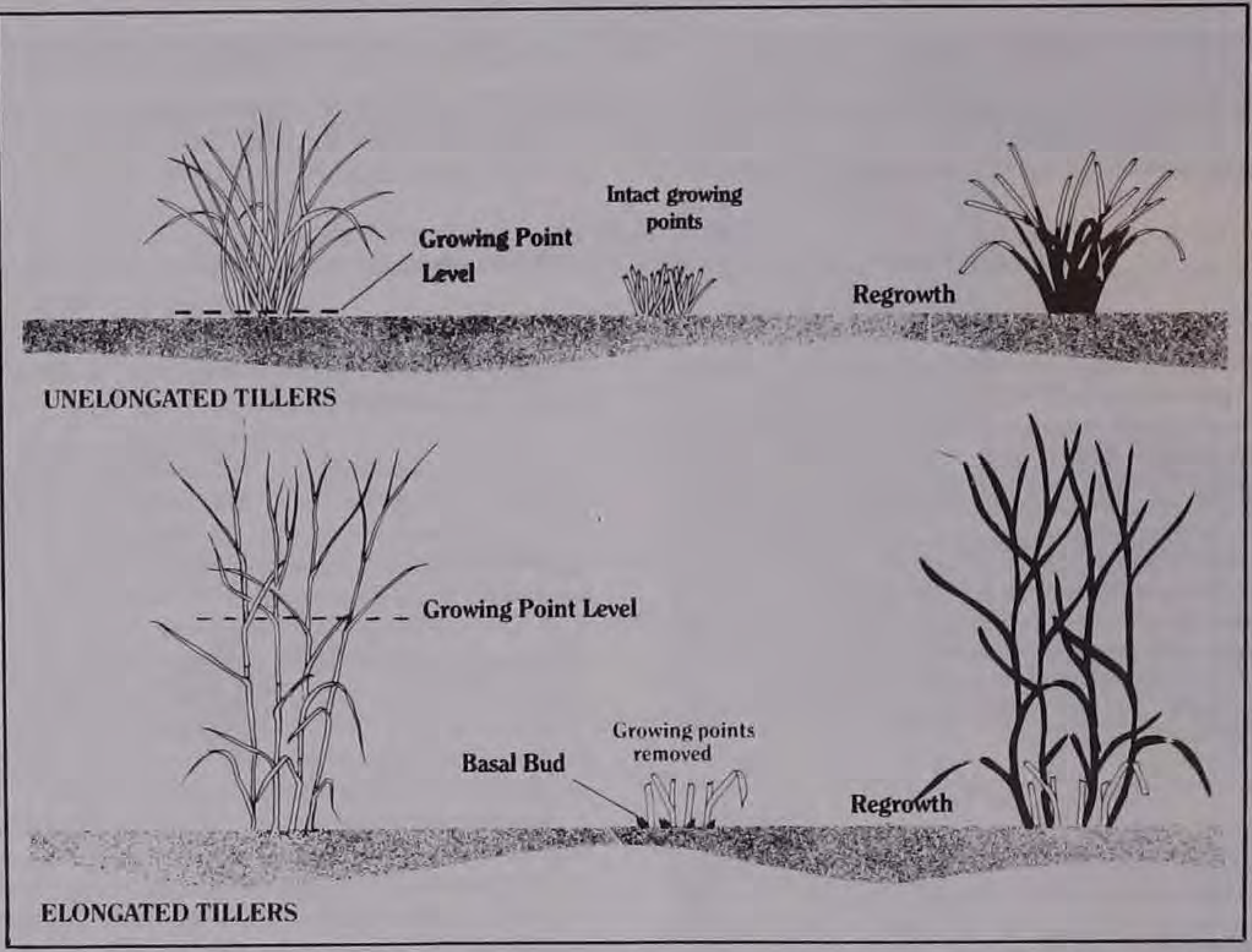

Figure 2. Regrowth of a grass from intact growing points compared to regrowth from basal buds (adapted from Moser et al. 1985).

RESULTS AND DISCUSSION

My results support the hypothesis that smooth brome tiller density would be significantly reduced if burning occurred after tiller elongation began. Burning in mid-May, when tillers were elongating, and in late May, at tiller heading, reduced fall tiller density by about 50% when compared to the control (Figure 3). There was no significant difference in fall tiller density between control plots and plots burned in early spring, when tillers were emerging. Reports from several natural areas are consistent with these findings. In eastern South Dakota, Blankespoor (1987) reported no substantial reduction in smooth brome in plots burned in late April, but a reduction did occur in plots burned in May. At Pipestone National Monument, Becker (1989) found cool-season grasses, Kentucky bluegrass (*Poa pratensis* L.) and smooth brome, decreased only 10% after five years of annual burns, generally conducted from mid- to late April.

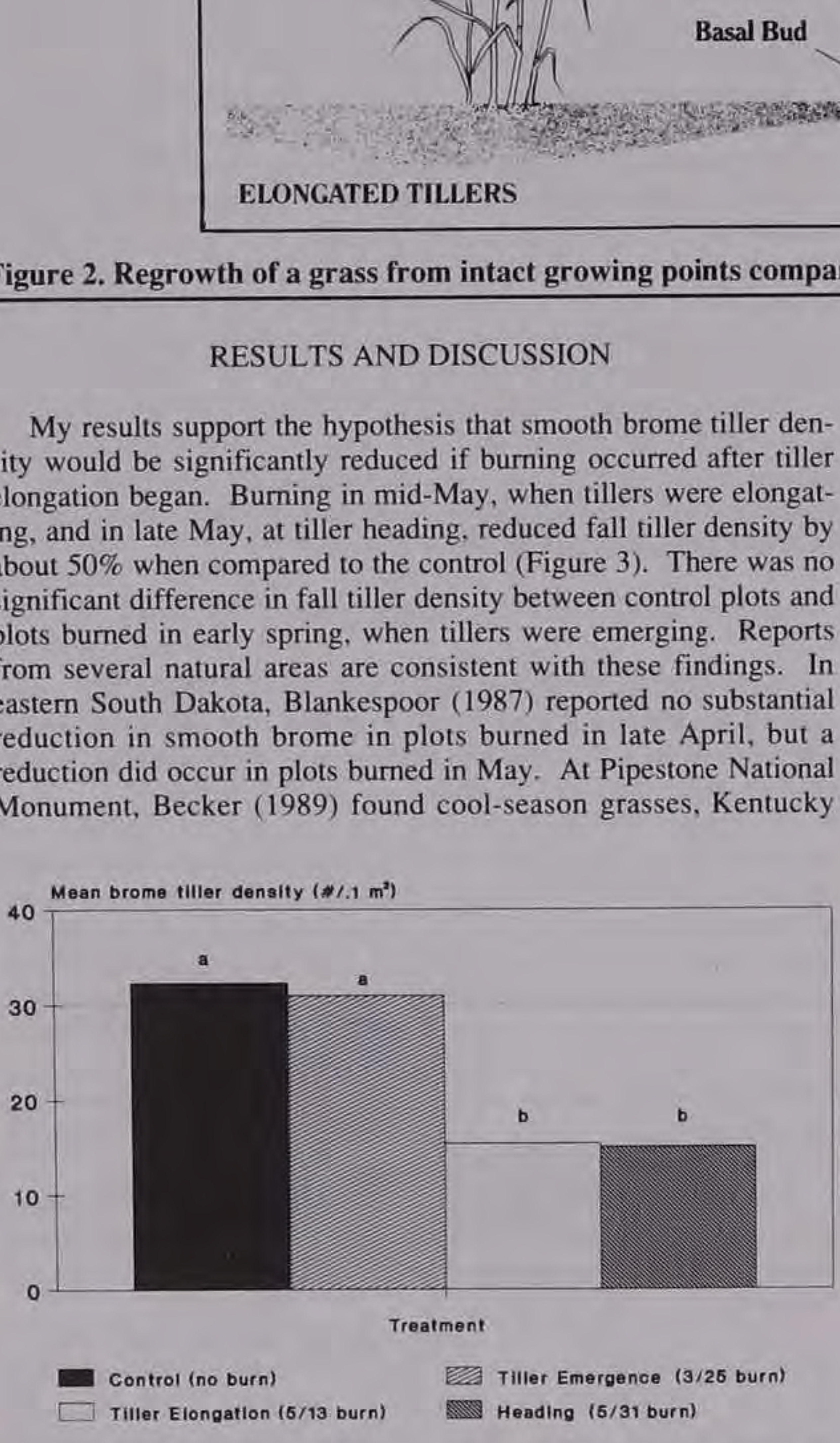

Figure 3. Mean smooth brome tiller density (#/0.1 m²) following different burning dates in 1989 at Mead, Nebraska. Means having the same letter are not significantly different (P>.05) according to Duncan's multiple range test.

Prescribed burns such as these fail to reduce smooth brome when they are conducted too early. Observations at Mead indicate that tiller elongation occurs after the period when prescribed burning is generally completed. In 1989, tillers did not begin to elongate until 7 May (Figure 4); by 14 May most tillers were elongating. Managers of northern prairies tend to burn early (usually before the end of April) for a number of reasons, including manpower and equipment availability, avoidance of visitor-use disruptions, and the perception that if you don't burn early, the vegetation will become too green to burn. However, Bragg (1982) and Higgins (1986) have shown that prairie vegetation can and does burn during late spring and summer. Although smokey, plots in my study burned very well in late May.

Managers are also concerned about the effects of late burns on native species. Big bluestem is the dominant native species throughout much of the tallgrass prairie and co-dominant with smooth brome at Mead. Late-spring burning has been reported to increase the density of big bluestem flower culms (Town and Owensby 1984). In a companion study at Mead, an increase in big bluestem flower culm density was greatest following a 13 May burn (Figure 5). This effect was coincident with a significant decrease in smooth brome tiller denstiy.

Since smooth brome phenology differs latitudinally throughout its range, managers cannot burn on a set calendar date. Managers need a site-specific method to determine if smooth brome is morphologically susceptible to fire. Although examing tillers for an above-ground node is an accurate means to determine if elongation is occurring, it is tedious. Becker (1989) used plant height as a management trigger but found burning smooth brome tillers at 10-15 cm or less in height resulted in only a small stand reduction after five years. In this study, on 7 and 14 May, the difference in mean tiller height for elongated and unelongated tillers was small (5 cm): thus, determining a burn date based on tiller height would have

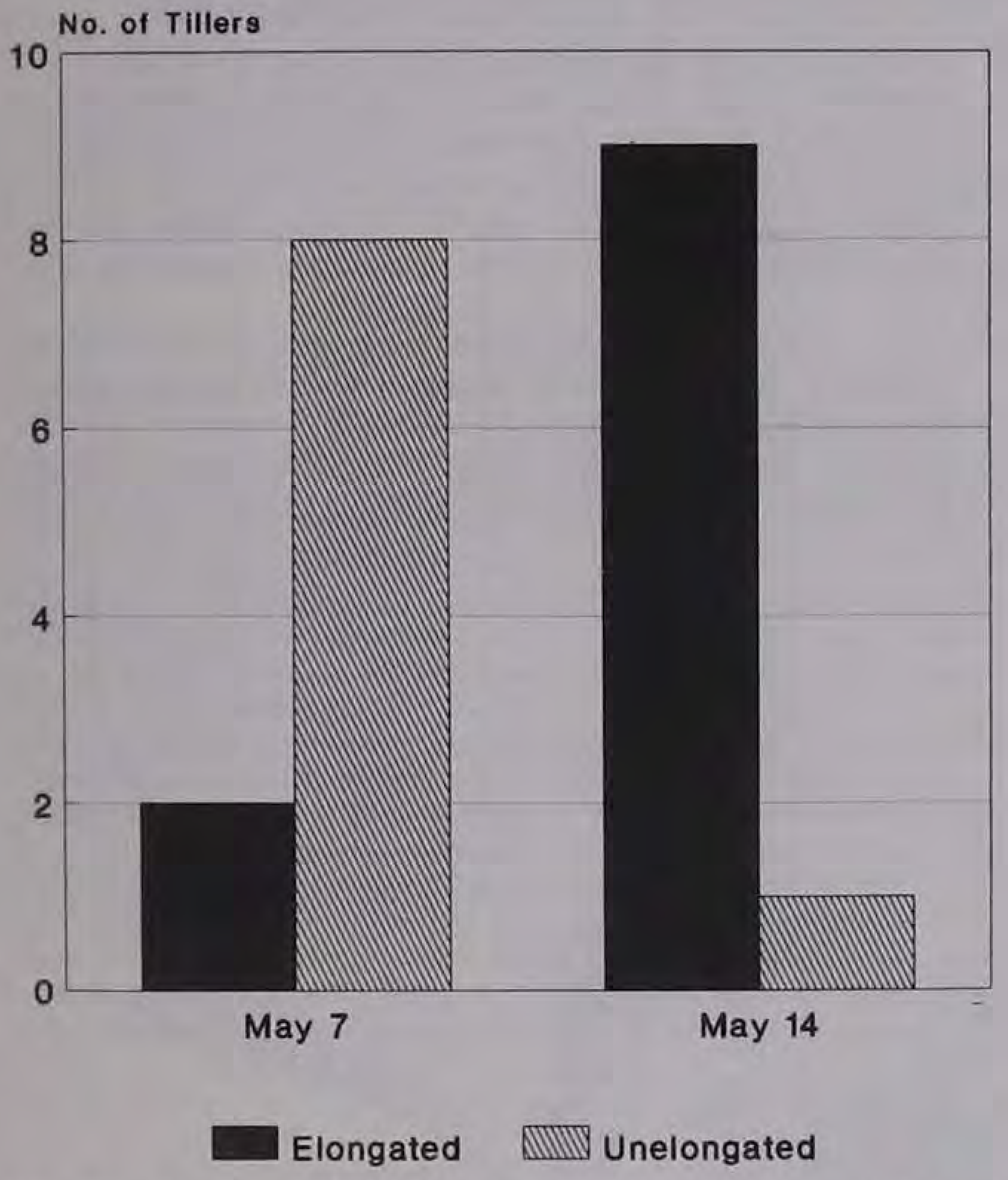

Figure 4. Numbers of elongated and unelongated smooth brome tillers 7 and 14 May 1989, at Mead, Nebraska.

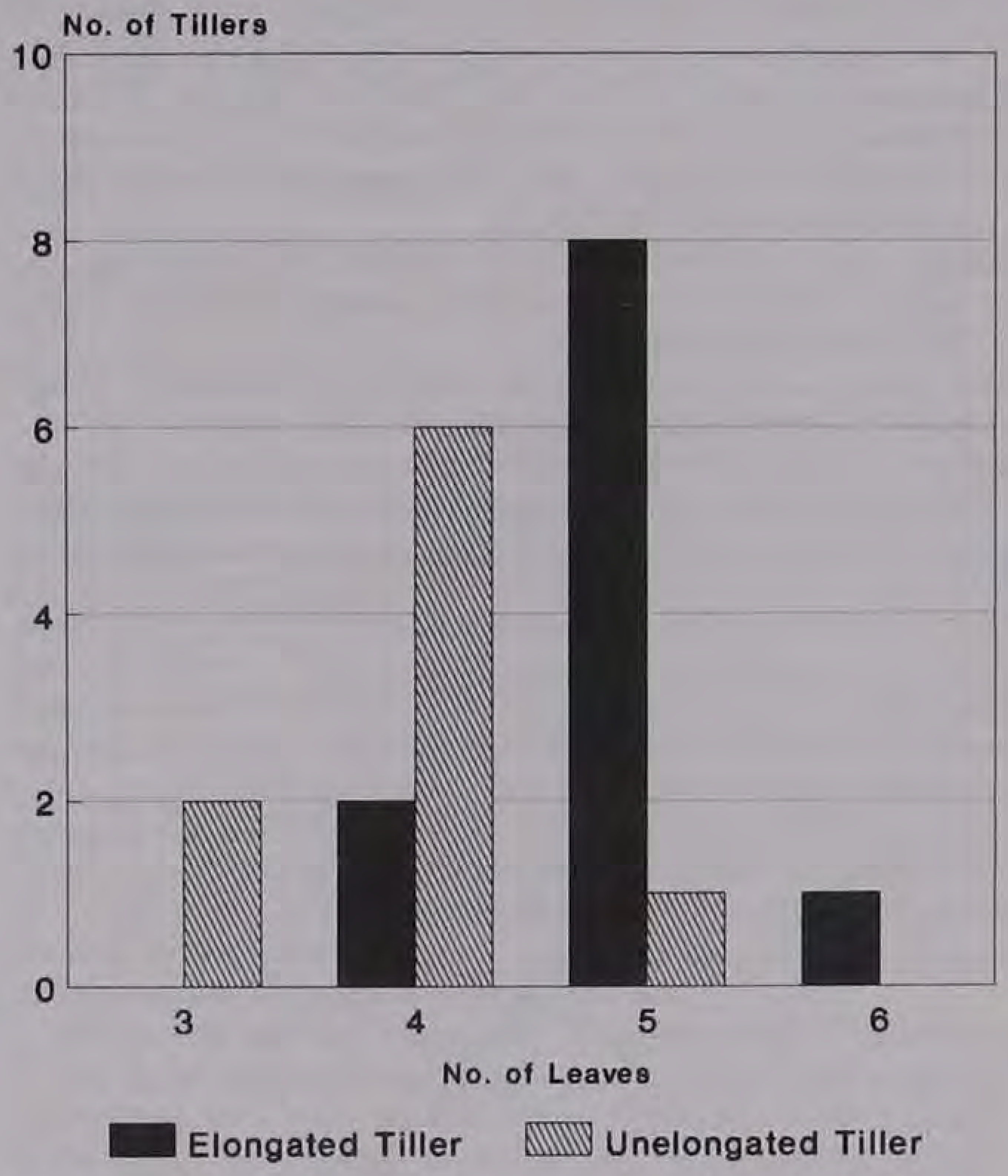

Figure 6. Leaves per elongated and unelongated smooth brome tillers on 7 and 14 May 1989 at Mead, Nebraska.

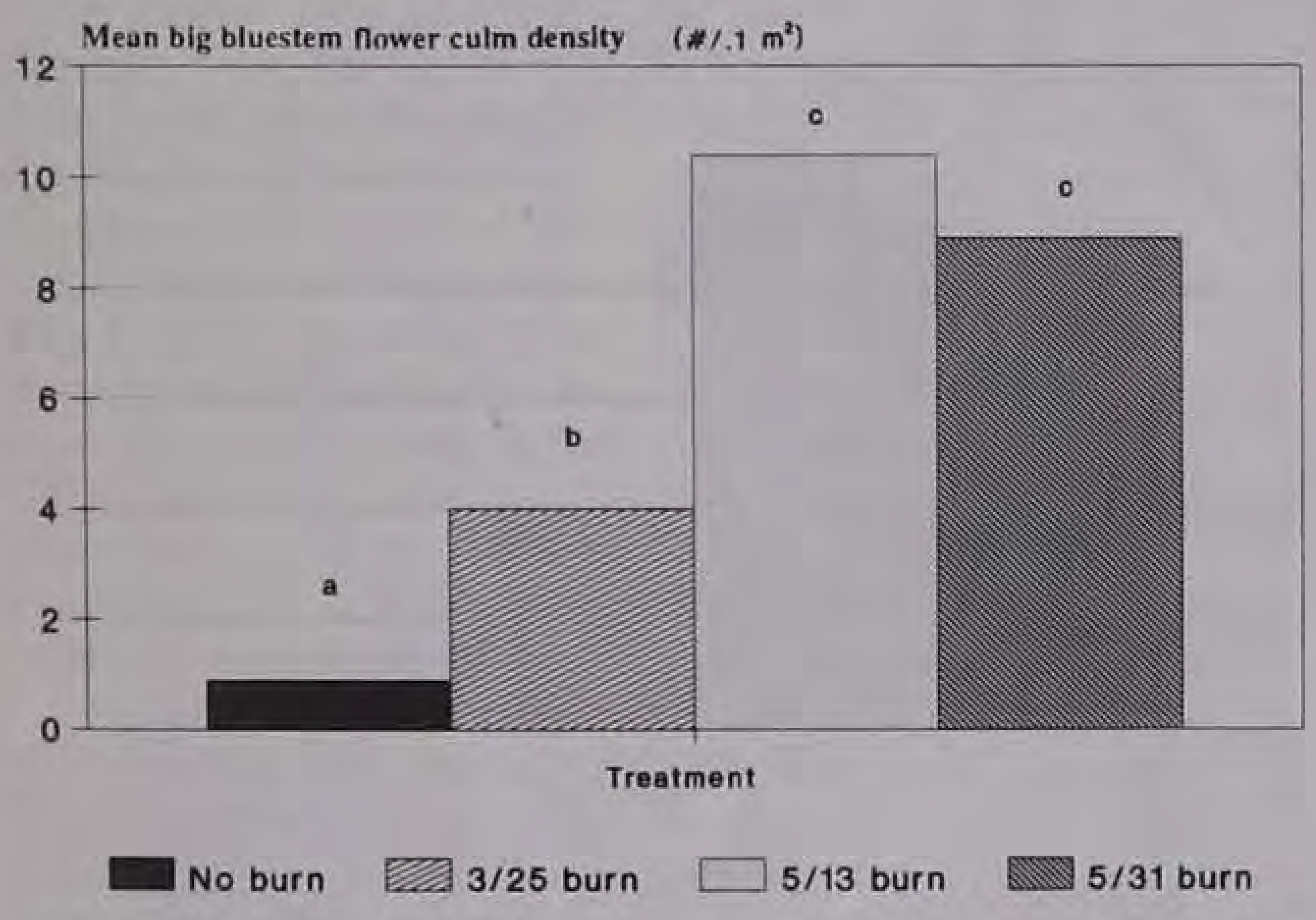

Figure 5. Mean big bluestem flower culm density (#/0.1 m²) following different burning dates in 1989 at Mead, Nebraska. Means having the same letter are not significantly different. (P>.05).

been difficult. The number of green leaves per tiller may be a better diagnostic characteristic for setting a burn date. My study results showed unelongated tillers generally had fewer than five green leaves; elongated tillers had five or more (Figure 6).

CONCLUSIONS

Results of this study suggest that burning smooth brome during tiller elongation (mid-spring and later), when the growing point is exposed, can significantly reduce fall tiller density. Also, big bluestem, a native prairie dominant, is enhanced rather than diminished by late-spring burns. Burning early, at tiller emergence, when the growing point is at or below ground, has no detrimental effect on smooth brome.

Structural (morphological) changes occur as grass tillers develop. In order to make sound fire management decisions, managers need to know the relevant morphological characteristics of the plant or plants they are targeting for control. For smooth brome, the number of green leaves per tiller is an easily observed indicator of plant susceptibility to fire.

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EFFECTS OF SPRING FIRE TIMING ON PASQUE-FLOWER (*ANEMONE PATENS*) FLOWER-BUD SURVIVAL

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Abstract. To quantify the effect of spring burning on pasque-flower (*Anemone patens* L.) flower-bud survival, a population of approximately 200 pasque-flower plants was subdivided into four units. One unit was left unburned as a control, while the other three were burned for five consecutive years at various times in the spring ranging from 18 days before to 8 days after the first blooming of pasque-flowers. It was found that the earlier the burn, the greater the flower-bud survival (linear regression significant at P = .04 level). However, the area burned latest each year, at the peak of flowering, still sustained a 15% to 20% flower-bud survival rate. This survival was thought to be due to late emerging buds. Years of late frost and high herbivory pressure proved to be exceptions to the general finding of greater bud survival with earlier burning. In years of late frost and high herbivory pressure, the rate of survival to seed set was actually higher on the late-burn plot. It is speculated that herbivores were attracted to sites burned early in the spring. Thus, more flowers were eaten, and, therefore, fewer seeds were produced on early-burned areas than on late-burned areas during years of high herbivore numbers. It is also speculated that staggered bud emergence is a strategy for coping with late frosts, spring fires, or both.

INTRODUCTION

Spring burning is a common management practice on prairie remnants, and it often occurs after early-blooming forbs, such as pasque-flower (*Anemone patens* L.), have emerged. The effect these spring fires have on early-blooming forbs is partly documented in the literature (Anderson and Bailey 1980, Ehrenreich and Aikman 1963, Henderson 1981, Henderson 1992, Leoschke 1986, Lovell et al. 1983, Pemble et al. 1981, Richards and Landers 1973), but much is still unknown.

Late-spring fires have been found to eliminate flower production of early-blooming species, such as prairie violet, *Viola pedatifida* G. Don; blue-eyed grass, *Sisyrinchium campestre* Bickn.; heart-leaved golden Alexander, *Zizia aptera* (Gray) Fern; and Valerian, *Valeriana ciliata* T.& G. (Henderson 1981, Lovell et al. 1983). This loss of flowers, however, does not necessarily translate into reduced vigor or population decline. For example, late-spring burns 8 out of 10 years did not reduce populations of prairie violet or blue-eyed grass in a Wisconsin prairie (Henderson 1992).

The effect of early-spring fires on early-blooming forbs appears to be less dramatic and more variable than that of late-spring fires. The responses have been reported to range from slightly negative to highly positive. Leoschke (1986) found shooting star (*Dodecatheon meadia* L.) flowering to be reduced 15% to 60% by early-spring fires. Lovell et al. (1983) found early-spring burns reduced flower production in Valerian, as well. In all other reports, species have shown neutral to positive responses to early burns. Heart-leaved golden Alexander and hoary puccoon, *Lithospermum canescens* (Michx.) Lehm, have exhibited both neutral and positive flowering responses (Ehrenreich and Aikman 1963, Lovell et al. 1983, Pemble et al. 1981). Prairie violet has shown no change in flowering (Henderson 1981, Lovell et al. 1983), but increases in cover and biomass have been observed (Lovell et al. 1983, Richards and Landers 1973). Blue-eyed grass; yellow stargrass, *Hypoxis hirsuta* (L.) Coville; and golden Alexander, *Zizia aurea* (L.) W.D.J.Koch, all have exhibited increases in flowering (Henderson 1981, Lovell et al. 1983, Pemble et al. 1981, Richards and Landers 1973). Golden Alexander was also reported by Richards and Landers (1973) to show an increase in cover and biomass.

How pasque-flower compares to these early-blooming species is not known. It blooms so early, four to six weeks ahead of the other species discussed here, that it is very difficult to extrapolate flowering responses from those species to pasque-flower. Only one study has reported specifically on pasque-flower's response to fire. This work was done by Anderson and Bailey (1980) in the aspen parklands of Alberta. They found pasque-flower canopy cover to be less on areas burned annually for 24 years than on comparable unburned controls. However, they found just the reverse response in pasque-flower frequency. This information suggests that the annual spring burning enhanced recruitment, that is, seedling establishment and survival, but reduced growth or vigor of pasque-flower. There appears to be no published data on what effect spring burning, or any other fire regime, has on flower production, flower survival, or seed production of pasque-flower.

Those with practical experience in burning areas with pasque-flowers know that established plants survive spring fires, even late-spring fires, very well and that flower production is often greatly reduced but rarely totally eliminated (R. A. Henderson, unpublished data). Given these observations and the lack of data on pasque-flower's flowering response to fire, this study was begun as a pilot project. Its objective was to quantify the effects of spring burn timing on pasque-flower flower-bud survival at a single site in south-central Wisconsin.

METHODS

A population of approximately 200 pasque-flower plants, covering approximately 0.7 ha of a 3.8 ha, dry to dry-mesic oak savanna/barren, was subdivided into four units. One unit was left as a small (0.01 ha) unburned control in the center of the population. It encompassed 22 plants. The other three units were burned with headfires, beginning in 1986, for five consecutive years at various times in the spring. The timing of the burns ranged from 18 days before to 8 days after the first blooming of pasque-flowers and fell roughly into three categories referred to as early, mid, and late (Table 1). The three burn units surrounded the control; each was contiguous to the control and the other two burn units. The number of pasque-flower plants encompassed by each unit were: 67 in unit one, 31 in unit two, and 74 in unit three.

Table 1. Timing of spring burns (relative to flower emergence) in each burn unit over the five years of the study.

	Burn units			*Control*
Year		*1*	*2*	*3*
1986	mid	late*	late*	no burn
1987	early	late*	late*	no burn
1988	early	mid	late	no burn
1989	early	early	late	no burn
1990	early	mid	late	no burn

*No data collected.

Each year at approximately two to three weeks after the last burn, all pasque-flower plants were visited once, and the fate of their flower-buds was determined. Buds and flowers were tallied into one of the following categories: 1) bud aborted or killed by fire or frost, 2) flower killed by fire, 3) flower eaten off, and 4) flower set seed. Data collection was timed (based on bi-weekly visits to the site) so that the fate of the last emerging buds could be determined, while the remains of killed buds or flowers were still evident. This proved to be a very effective technique. Fires did not completely consume green buds or flowers. Consequently, ample dried tissue was left behind to allow determination of flower stage at the time of fire, up to five or six weeks after the burn. Eaten flowers were also easy to determine, since the residual flower stalk remained alive and upright for a month or more after the grazing occurred. Records were also kept on the dates of the first and last flowers in the population.

The data were analyzed using linear regression to relate the timing (relative to pasque-flower phenology) of the fires to 1) the percentage of flower-buds alive post-fire (above data categories 3+4/1+2+3+4), 2) the percentage of all flower-buds surviving to seed set (above data categories 4/1+2+3+4), and 3) the percentage of post-fire flowers eaten by herbivores, primarily rabbits (above data category 3/3+4).

An additional analysis was run comparing plant size with bud survival to flowering stage in the late-burn unit. This was done by assigning plants to one of two categories—large, 6 or more flower-buds; or small, less than 6 flower-buds. Mean size for the population was 7. For each year, chi-square tests were run on 2 x 2 contingency tables of size versus bud survival.

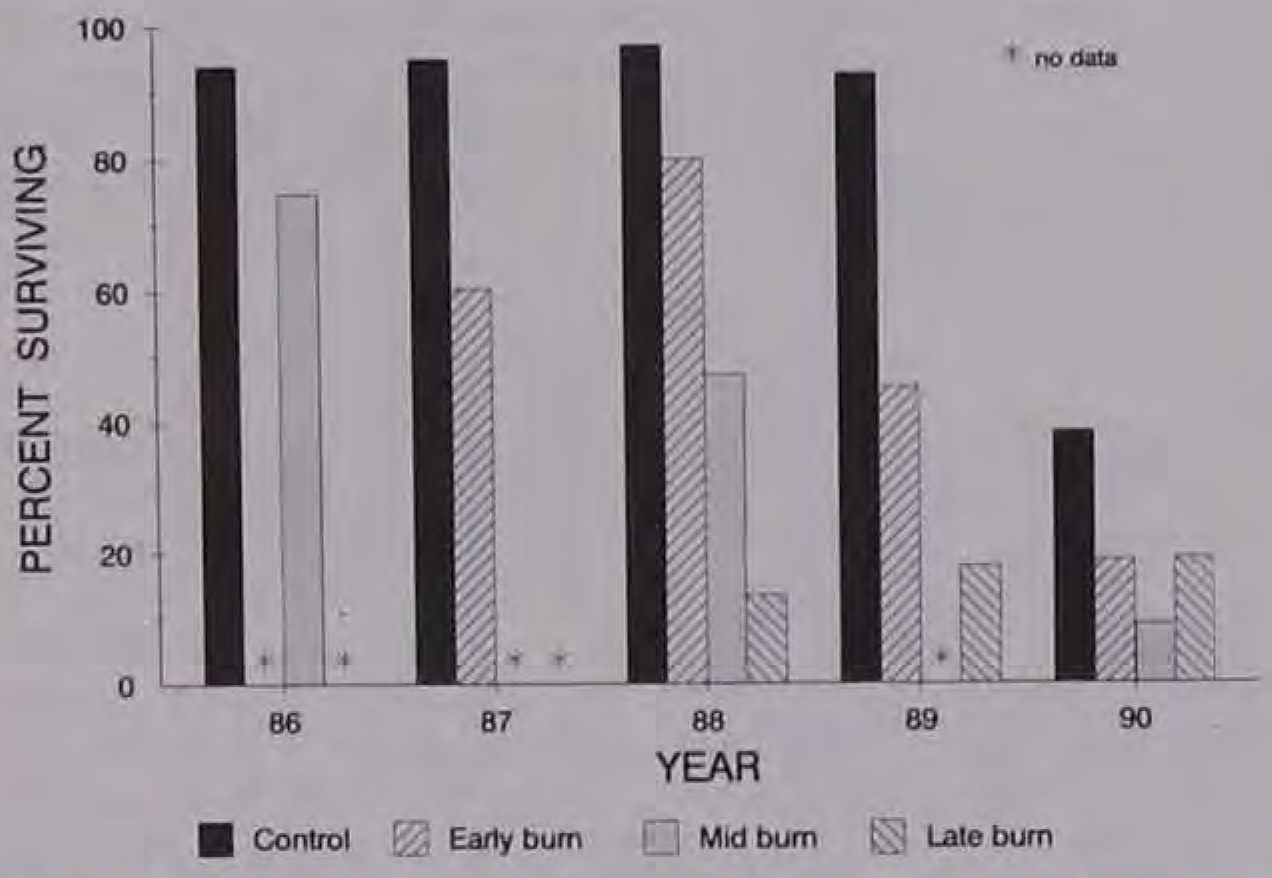

Figure 1. Percentage of flower-buds surviving to blooming stage.

RESULTS

The rate of flower-bud survival to the flowering stage was consistently higher on the unburned control than on the burn units (Figure 1). Survival rates on the control ranged from 93% to 97% in four out of five years. In 1990, however, survival was only 38%, but this was still 50% to 70% higher than that observed in the burn units.

The rate of flower herbivory was consistently low in the control, ranging from 0% to 5%. Herbivory rates in the burn units were far more variable, ranging from 0% to 91%. They varied from year to year and with the timing of the burns.

On the burned plots, a significant (P = .04) linear relationship was found between the timing of the burn and flower-bud survival (Figure 2). The earlier the burn, the higher the survival rate. Timing accounted for 43% of the observed variation. Outliers in the data (years 1986 and 1990) indicate that year effect and probably year/timing interactions contributed to the variation, as well. Unfortunately, the data set was not large enough for an adequate analysis of covariance.

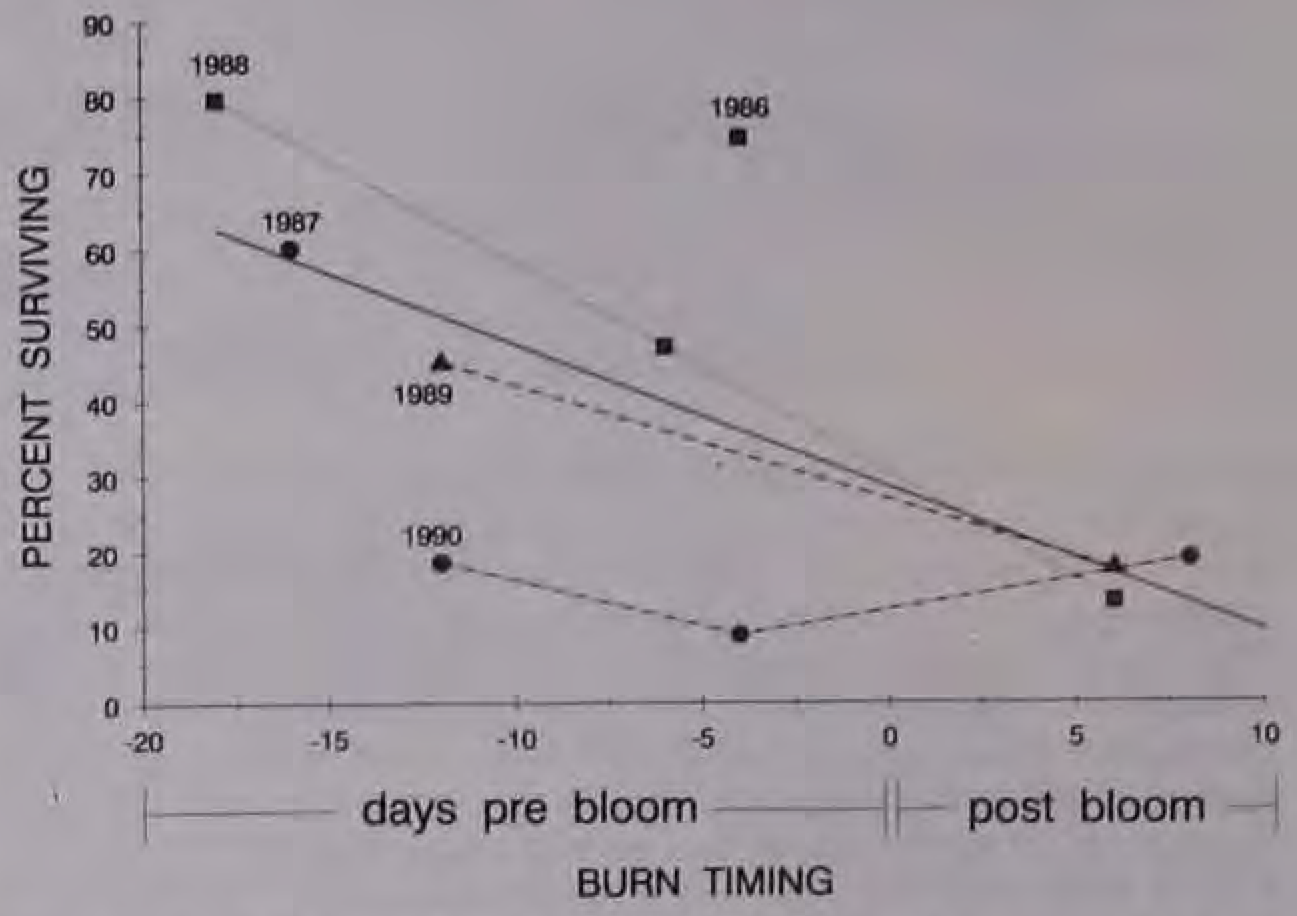

Figure 2. Effect of spring fire timing on the percentage of flower-buds surviving to flowering stage. The solid line is the best fit linear regression model ($R^2 = .428$). The model is significant at the P = .04 level. Burns in the same year are connected by dotted or dashed lines.

No general correlations were found between burn timing and post-fire herbivory rates or burn timing and survival to seed set. However, a possible year/timing interaction effect was apparent. For example, in years of high herbivore pressure (1987 and 1990), the late-burn plot lost proportionally fewer flowers to herbivores than the plots burned earlier (Figure 3). This in turn affected flower-bud survival to seed set (Figure 4) to the extent that the survival rate was 3 to 10 times higher in the late-burn unit than in the early- and mid-burn units during 1987 and 1990.

Flower-buds of large plants, with 6 or more buds, were found to survive the late fires at rates three to four times higher than buds in small plants. Chi-square P values were .0926 for 1988, .0003 for 1989, and .0012 for 1990. The blooming period of the study population ranged from 33 to 37 days (Table 2).

In two out of the five years, evidence of extensive winter vole (*Microtus* sp.) activity, surface runways, nests, and crown damage to bunch grasses and other plants, was noted in the control. However, little or no evidence of activity was found in the adjacent burned areas. During those high vole years, approximately one-third of the pasque-flower crowns within the control area were partially eaten by voles, eliminating flower-buds and severely damaging the plants. No such damage was detected in the adjacent burned areas.

Additional unquantified observations included 1) staggered flower-bud emergence, 2) individual flower longevity of approximately seven days, 3) leaf emergence in a given plant lagging approximately four weeks behind its first flower opening, and 4) no new plant establishment in the unburned control during the study, while at least some recruitment was observed in all burned units.

Table 2. Observed blooming periods of pasque-flower.

Year	*Dates*	*Total days*
1987	23 March - 24 April	33
1988	4 April - 8 May	35
1989	14 April - 19 May	36
1990	30 March - 5 May	37

DISCUSSION

Survival to Flowering Stage

It is not surprising that there was a linear correlation between burn timing and rate of flower-bud loss and that survival rates were always highest on the unburned control. Pasque-flower flower-buds frequently begin emerging from the ground one to two weeks prior to actual blooming (personal observation), making them susceptible to fire damage well before the actual blooming stage. Less predictable observations were 1) the consistent 15-20% flower-bud survival rates in burns occurring at or near the peak of flowering, and 2) the generally anomalous results observed in 1990, when no survival advantage was afforded to buds by early vs. late burning, and 85% less advantage was derived from no burning, compared to he previous four years.

It was apparent from frequent field observations that the presence of surviving flowers in the late burn plots was due mostly to ate emerging buds that were still near or below ground level, and hus protected, when the fire occurred. However, there was also vidence that on rare occasions emerged flowers did manage to survive, as well. No data was collected on bud emergence times. However, evidence in support of staggered emergence comes from the long blooming period that was observed (Table 2), which was pproximately four to five times the longevity of an individual flower.

Phenological variation among individuals probably contributed to this variance in bud emergence. However, most of the variance was probably due to staggered bud emergence within large, multiple-bud individuals. No direct data was collected that would support this contention. However, the finding that buds of large plants were three to four times more likely to survive to flowering stage than buds of small plants lends support to the idea. Given this evidence, large plants either 1) emerge later on average than small plants, 2) provide more protection to buds/flowers than small plants, or 3) exhibit staggered bud emergence. Based on field observations, I believe the staggered emergence option to be the dominant factor in determining bud survival rates.

The atypical bud survival observed in 1990 (Figure 2) was probably due to an unusually late, hard frost that occurred about the time the first pasque-flowers were opening. A likely mechanism is that litter provides protection against frost. Plots burned prior to the frost had no mulch layer to protect the emerging flower-buds. Thus, they suffered disproportionately more frost damage than plots that were still unburned at the time, both control and late burn plots. In 1990, the early- and mid-burn plots had survival rates well below those of other years and of the late-burn plot (mulch protected at time of frost), while rates on the late-burn plot remained comparable to the previous years. Litter, however, does not appear to provide total protection from late frosts. Even on the control plot, the survival rate was only 38% in 1990 compared to 92-97% in the other years. From the results of 1990, it appears that late frosts can equalize differences in bud survival between late burning and early burning, and even to some degree between late burning and no burning.

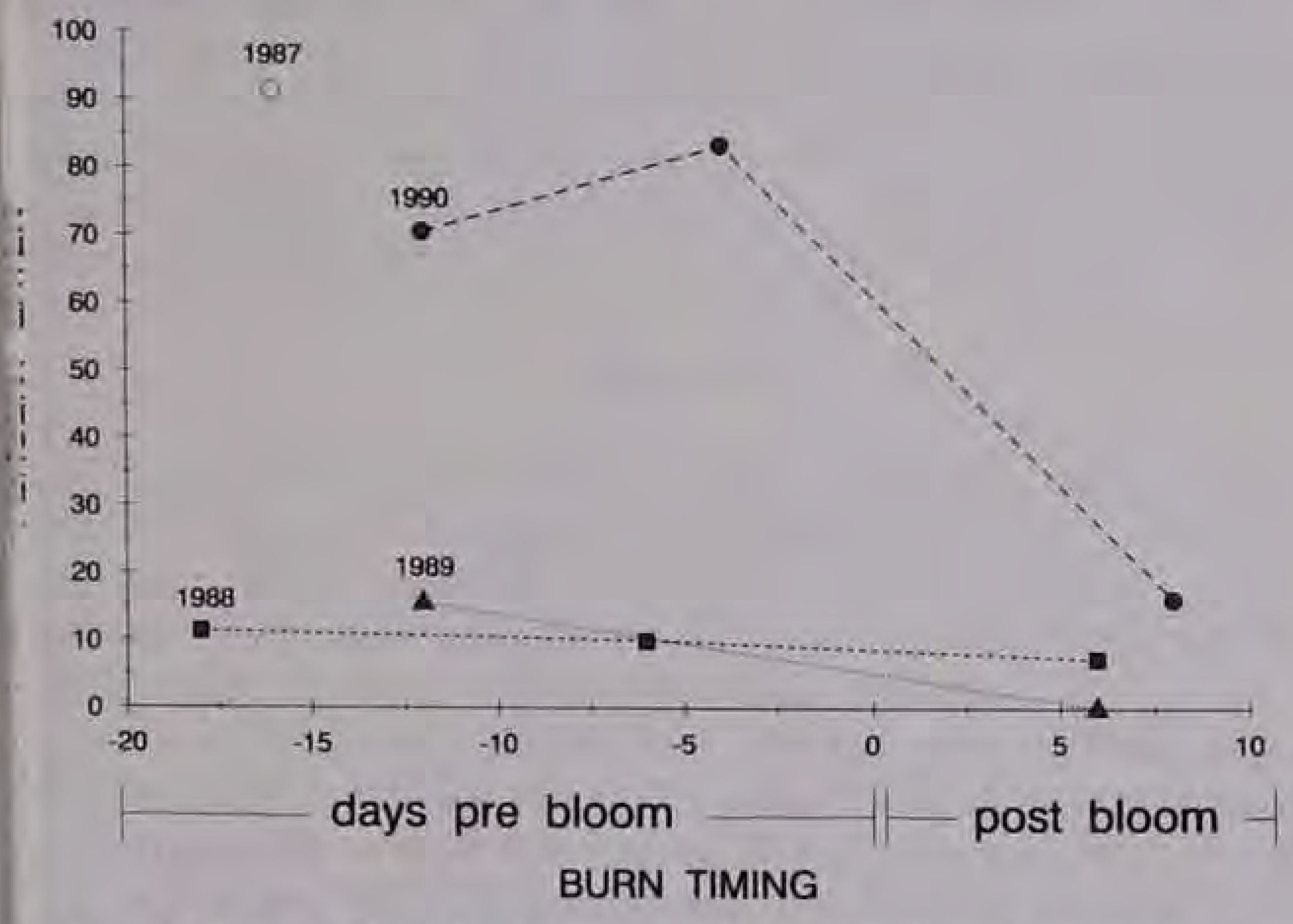

Figure 3. Effect of spring fire timing on the percentage of post-fire flowers lost to herbivores.

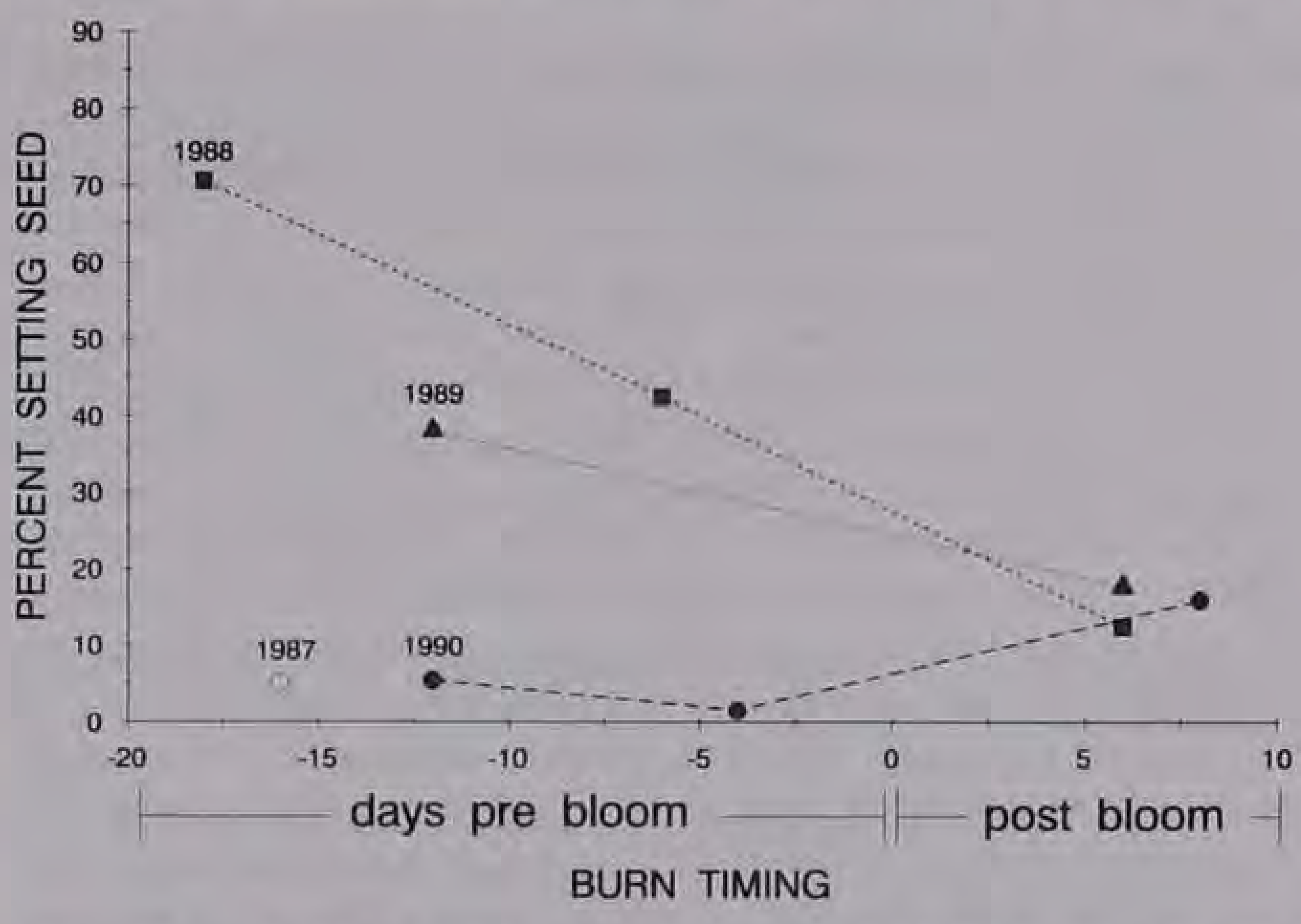

Figure 4. Effect of spring fire timing on the percentage of flower-buds surviving to seed set.

Staggered flower-bud emergence and delayed leaf emergence in pasque-flowers are two subjective observations of this study that warrant more conclusive documentation. If they prove to be real and consistent traits of the species, they may be important adaptations that allow pasque-flowers to do well in an environment of unpredictable spring fires and frost.

Survival to Seed Set

The percentage of flower-buds surviving to seed set appeared to be dependent upon interactions between burn timing and herbivory, primarily by rabbits. In years of low herbivore pressure (1988 and 1989), herbivory rates were similar across treatments (Figure 3). In those years, bud survival appeared to be solely a function of fire/frost damage. Therefore, early- and mid-burning resulted in more seed production than late-burning (Figure 4). In years of high herbivore pressure (1987 and 1990), herbivory rates were far higher on the early- and mid-burn plots (70% to 90%) than on the late-burn (16%) or unburned control (5%) plots. In those years, survival to seed set was actually higher on the late-burn plot than on the early- or mid-burn plots.

It appears that when herbivore pressure was high, grazing became concentrated on the areas burned early in the spring. Earlier green-up on these areas is a probable cause for this grazing concentration, especially grazing on pasque-flowers, which are among the first plants to emerge. By the time the late-burned areas became attractive to grazers, there was ample forage on all the plots, thereby dispersing the grazing pressure.

Unburned Control

The fact that seed production (% of flower-buds surviving to seed set) was consistently greater on the unburned control suggests that lack of fire or infrequent burning may be beneficial to pasque-flower populations. However, two subjective observations made in the unburned control during the course of this study—1) damage from voles and 2) lack of recruitment—indicate that litter accumulation in the absence of fire may negate the benefit of greater seed production.

The voles apparent preference for the unburned control over the burned areas is in character with their known behavior. Voles have a clear preference for thick accumulations of litter, and frequent burning is known to suppress their numbers (Kaufman et al. 1990).

The apparent lack of pasque-flower recruitment in the unburned control may be the result of the plot's thick accumulation of litter interfering with seedling establishment. The litter may have prevented seeds from coming in contact with soil, or it may have simply shaded out the seedlings. These and other negative effects of litter on seedling establishment have been speculated upon in the literature (Anderson and Bailey 1980, Knapp and Seastedt 1986, Rapp and Rabinowitz 1985), but they are not well documented. Studies with direct evidence are very few. Goldberg and Werner (1983) reported litter cover to have a negative effect on goldenrod (*Solidago* spp.) seedling establishment, and Glenn-Lewin et al. (1990) found litter removal to benefit seedling establishment in wet, but not dry years. The lack of information on the effect of litter on seedling establishment and survival in prairie is a major gap in our understanding of fire effects and needs further investigation.

It appears that maximum benefit to pasque-flower populations would come from conditions that minimize litter accumulation while maximizing seed production. Frequent mid- to late-summer burning or grazing, after seed fall; frequent late-fall burning; or spring burning every two to three years may provide those conditions and need to be studied. There is already some evidence that late-fall burning may benefit early-blooming forbs (Henderson 1992), and pilot work currently being done on the effects of grazing and summer burning suggest that these management practices may increase plant species diversity in prairie (Adams et al. 1982, Collins and Gibson 1990, Henry F. Howe, University of Illinois at Chicago, unpublished data), including cool-season forbs. Circumstantial evidence indicating that grazing may favor pasque-flowers can be seen in many Wisconsin prairie remnants where dense pasque-flower populations are often associated with former grazing (personal observation).

ACKNOWLEDGEMENTS

I thank Paul Rasmussen and Lisa Hartman for their statistical and editorial review of this paper. I also thank Brian Dhuey for his work on the computer graphics.

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TEN-YEAR RESPONSE OF A WISCONSIN PRAIRIE REMNANT TO SEASONAL TIMING OF FIRE

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Abstract. Four test plots were established in a high quality prairie remnant in south-central Wisconsin. Within each plot, 20 permanent quadrats (0.25 m^2) were monitored from 1980 to 1989 to determine the effects of three different burn treatments on the vegetation. The treatments were late fall, early spring, and late spring burns conducted repeatedly to the same plots for 8 out of the 10 years. Data collected from each quadrat included the number of individuals or ramets of all forbs and bunch-grasses and the presence or absences of sod-forming grasses. A severe drought from May through July in 1988 caused a significant (17%) decline in species density and a drop in diversity from 20.98 to 17.94 (reciprocal of Simpson's index of diversity). The drought caused significant reductions in numbers of *Sisyrinchium campestre* Bickn. and *Viola pedatifida* G. Don. The late spring burn plot was the only treatment plot to exhibit a significant change in plant composition. By the 10th year its composition was no longer similar to the other plots, and its species density had declined 29%. Most of the change was due to declines in *Carex* sps. (60%), *Poa pratensis* L. (99%), *Euphorbia corollata* L. (73%), *Panicum leibergii* (Vasey) Scribner (99%), and P. *oligosanthes* Schultes (93%). Only one species, *Stipa spartea* Trin., increased in the late spring burn plot, as it did in the other burn plots, while remaining stable in the control.

INTRODUCTION

Prescribed burning is widely used as a management tool in tallgrass prairie. Yet, much is unknown about its effect on prairie vegetation, especially long-term effects, effects on forbs, and effects of seasonal timing of fire. Four long-term projects have been reported in the literature, but none are from the eastern three-quarters of the tallgrass prairie range. Anderson and Bailey (1980) reported the effects of 24 years of annual spring burning in an Alberta mid-grass prairie. Towne and Owensby (1984) discussed the effects of 56 years of burning in a northeastern Kansas tallgrass prairie. Svedarsky et al. (1986) reported the effects of 13 years of annual spring burning on a degraded prairie in northwestern Minnesota. Several authors (Abrams et al. 1986, Abrams and Hulbert 1987, Gibson and Hulbert 1987, Abrams 1988) have reported on a 15-year study of fire effects at Konza Prairie Research Natural Area in Kansas. The Towne and Owensby (1984) study was the only project to investigate seasonal timing of fire, but their data on forbs was limited.

The objective of this project was to begin vegetation data collection on long-term effects of seasonal timing of fire on forbs and grasses in eastern tallgrass prairie. In 1979, permanent test plots were established in three prairie stands. This paper reports the compositional changes in one of these stands after 10 years.

METHODS

The study was conducted on a high quality, dry to dry-mesic (Curtis 1959) prairie remnant in south-central Wisconsin. The site is located on a south-facing slope of 23 degrees, and the soil is a Dunbarton silt loam over glacial till (Glocker and Patzer 1978). Baseline plant frequency data are presented in Table 1.

Four test plots, each 120 m^2 (20 m by 6 m) and separated by 1.5 m buffer strips, were located side-by-side. These plots were judged to be comparable to each other based on pre-treatment comparisons of the vegetation using Sorensen's index of similarity (Curtis 1959, Mueller-Dombois and Ellenberg 1974). Index values ranged from 0.83 to 0.90. The indices were calculated using vegetation data from 20 quadrats (0.25 m^2) per plot, located in a stratified-random method.

Different burn treatments were randomly assigned to three of the plots. These included late fall, early spring, and late spring burns. The remaining plot was left unburned. There was no replication of treatments. The burns were applied repeatedly to the same plots for 8 out of the 10 years: 1980 to 1982 and 1985 to 1989. Late fall burns occurred between 15 November and 10 December, approximately 60 days after the first hard freeze. Early spring burns occurred between 23 March and 10 April, approximately one to two weeks before the first opening of pasque flowers (*Anemone patens* L.). Late spring burns occurred between 7 May and 21 May, approximately two weeks after the first blooming of prairie violet (*Viola pedatifida* G. Don) and blue-eyed grass (*Sisyrinchium campestre* Bickn.).

Table 1. Baseline composition of study area - top 20 species.

Species		*% Frequency*[1]
Sorghastrum nutans	(Indiangrass)	98
Bouteloua curtipendula	(Side-oats grama)	95
Euphorbia corollata	(Flowering spurge)	86
Andropogon scoparius	(Little bluestem)	74
Helianthus laetiflorus	(Showy sunflower)	68
Panicum leibergii	(Leiberg's panic-grass)	66
Poa pratensis	(Kentucky bluegrass)	66
Andropogon gerardi	(Big bluestem)	64
Physalis virginiana	(Ground cherry)	49
Amorpha canescens	(Leadplant)	48
Panicum oligosanthes	(Few-flowered panic-grass)	46
Viola pedatifida	(Prairie violet)	45
Sisyrinchium campestre	(Blue-eyed grass)	44
Asclepias verticillata	(Whorled milkweed)	36
Carex umbellata	(Umbel sedge)	35
Aster azureus	(Sky-blue aster)	31
Comandra umbellata	(Bastard-toadflax)	25
Stipa spartea	(Needle-grass)	21
Sporobolus heterolepsis	(Prairie dropseed)	19

[1] Based on 80 (0.25 m^2) quadrats sampled in a stratified-random method.

Vegetation changes were measured using 20 permanently marked, 0.25 m^2 quadrats per plot. Species presence and density (number of individual plants or ramets) were recorded for each quadrat during June. Sod-forming grasses were noted only as present or absent. Bunch-forming grasses were identified and tallied as discrete individuals (*Note:* Determining individuals was generally a straightforward task, but on occasion it became subjective with old, large clumps that were in advanced stages of disintegrating into separate units). Data were collected on grasses only, in 1982 and on grasses and forbs in 1980, 1981, 1983, 1987, and 1989.

Comparisons were made among the plots and within the plots over time on the density (numbers per 0.25 m^2) or frequency of occurrence of all species with an initial frequency of 20% or more. In addition, comparisons were made of species richness, total number of species from all quadrats combined; vegetation similarity, Sorensen's index of similarity; species density, mean number of species per 0.25 m^2; and species diversity, reciprocal of Simpson's index of diversity (Ludwig and Reynolds 1988). Density data were analyzed with one-way ANOVA using the Tukey procedure for pairwise comparisons among means. Frequency data were analyzed with chi-square tests. Because the burn treatments were not replicated, the ANOVA used within-plot variability as the measure of error. Such an analysis provides a valid statistical method of determining differences among plots, but it cannot conclusively demonstrate that the treatments were the cause of any observed differences.

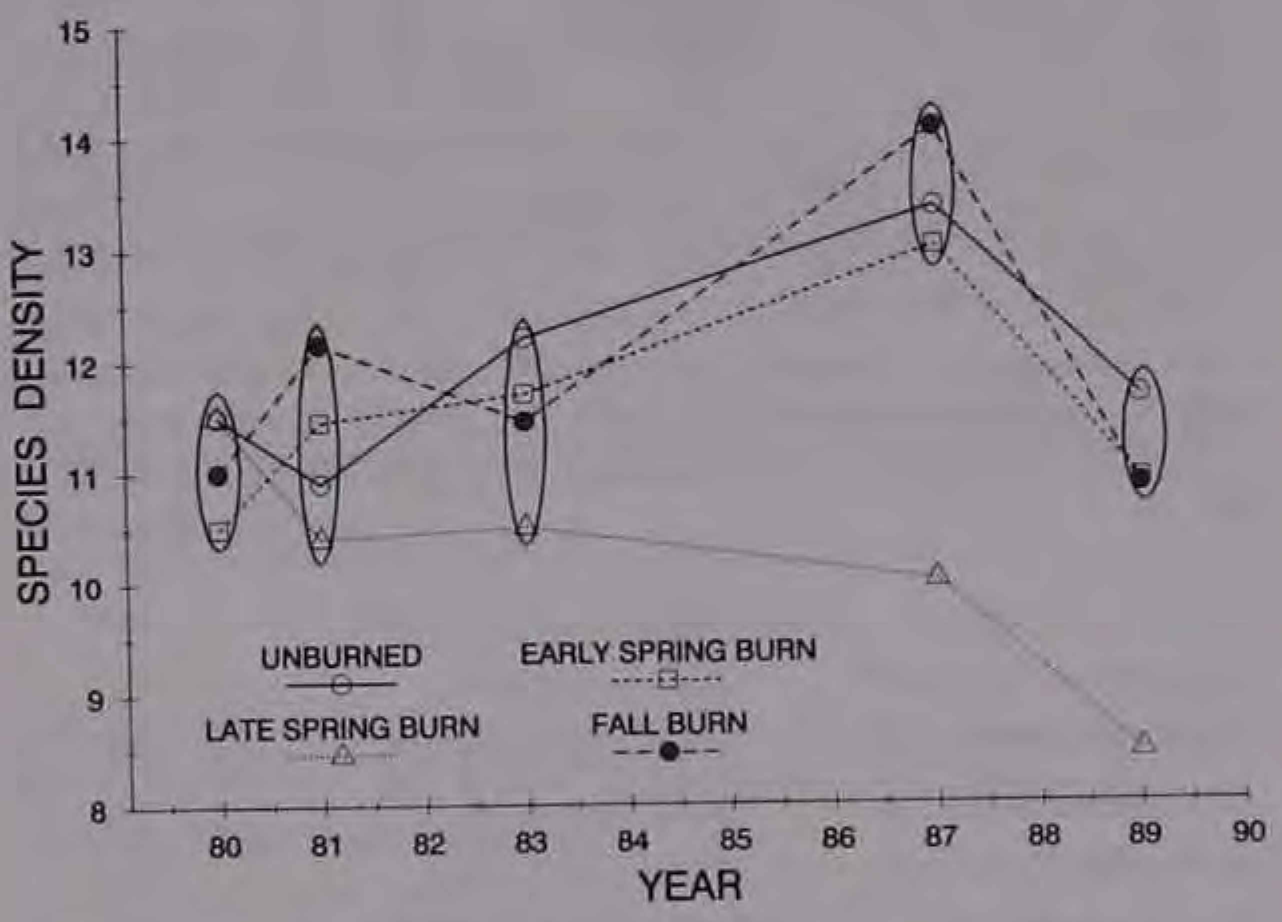

Figure 1. Species density (mean number of species per 0.25 m^2) in treatment plots over time. Circled points are not significantly different from each other at the $P < .05$ level.

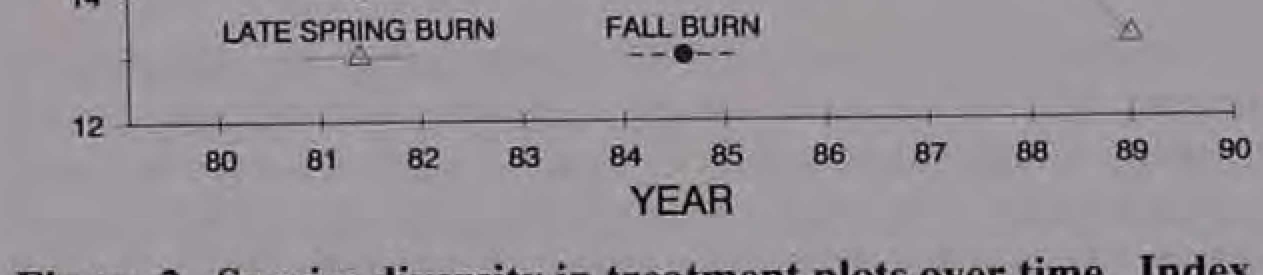

Figure 2. Species diversity in treatment plots over time. Index values are the reciprocal of the Simpson's index of diversity (Ludwig and Reynolds 1988).

Table 2. Drought effects. Percent change in abundance from 1987 to 1989.

Species	Unburned	Burned Late fall	 Early spring	 Late spring
Helianthus laetiflorus	n[a]	+165[2]	+91[2]	-60[2]
Amorpha canescens	n	n	n	n
*Andropogon gerardi**	n	n	n	n
Andropogon scoparius	n	n	n	n
Asclepias verticillata	n	n	n	n
Aster azureus	n	n	n	n
*Bouteloua curtipendula**	n	n	n	n
Carex umbellata	n	n	n	n
Comandra umbellata	n	n	n	n
Sporobolus heterolepsis	n	n	n	n
Stipa spartea	n	n	n	n
*Sorghastrum nutans**	n	-25[1]	n	n
Panicum oligosanthes	n	-47[1]	n	n
Physalis virginiana	n	-57[1]	n	n
Euphorbia corollata	-45[2]	-21[1]	-37[1]	n
Panicum leibergii	n	-56[2]	-43[2]	-100[1]
*Poa pratensis**	n	-73[2]	-57[2]	-100[2]
Viola pedatifida	-38[1]	-80[2]	-33[1]	-33[1]
Sisyrinchium campestre	-100[1]	-96[2]	-90[2]	-70[1]

[a] No significant change.
*Based on frequency of occurrence.
[1] Significant at $P < .10$.
[2] Significant at $P < .05$.

RESULTS AND DISCUSSIONS

Drought Effects

A severe spring/summer drought occurred in 1988. During May, June, and July, the precipitation was 65% to 70% below normal, and the mean monthly temperatures were 2 C to 3 C above normal (National Climatic Data Center 1989).

This drought coincided with significant declines in species density and diversity in all treatment plots (Figures 1 and 2). The mean number of species per quadrat for all plots combined changed from 12.6 in 1987 to 10.5 in 1989 ($P < .0001$). Responses of individual species to the drought are presented in Table 2.

Shallow-rooted, early-blooming species—prairie violet, blue-eyed grass, Kentucky bluegrass (*Poa pratensis* L.), Leiberg's panic-grass [*Panicum leibergii* (Vasey) Scribner], few-flowered panic-grass (P. *oligosanthes* Schultes), and ground cherry (*Physalis virginiana* Mill.)—declined the most during the drought. This was probably due to the drought's early spring onset. Early-blooming species are normally most active in spring and fall with mid-summer dormancy being a common occurrence. Thus, they are well adapted to mid-summer, but not spring, droughts.

Prairie violet and blue-eyed grass exhibited drought related declines in all plots. The declines of other species, however, were associated only with apparent synergistic effects of drought and fire. For example, Kentucky bluegrass and Leiberg's panic-grass declined in all burn plots, but not in the unburned control. Few-flowered panic-grass and ground cherry responded negatively to the drought only in the fall burn plot. Indian grass, *Sorghastrum nutans* (L.) Nash, may have been affected by the drought in the fall burn plot, as well. Its frequency declined 25% (significant at $P < .10$ level) from 1987 to 1989 in the fall burn plot, while remaining stable elsewhere.

Table 3. Fire effects. Percent change in abundance in burned and unburned plots after 10 years.

		Burned		
Species	*Unburned*	*Late fall*	*Early spring*	*Late spring*
Stipa spartea	n[a]	+2200[3]	+380[3]	+800[3]
Andropogon scoparius	n	+40[3]	+125[3]	-36[3]
Aster azureus	n	+83[3]	n	n
Viola pedatifida	-50[1]	n	-50[1]	-65[3]
Physalis virginiana	-91[2]	-79[2]	n	n
Sisyrinchium campestre	-100[2]	n	n	n
*Andropogon gerardi**	n	n	n	n
Amorpha canescens	n	n	n	n
*Bouteloua curtipendula**	n	n	n	n
Comandra umbellata	n	n	n	n
*Sorghastrum nutans**	n	n	n	n
Asclepias verticillata	+380[2]	n	n	+94[2]
Helianthus laetiflorus	+280[2]	+470[2]	+127[2]	n
Carex umbellata	+230[1]	+50[1]	+140[2]	n
Sporobolus heterolepsis	n	n	n	-100[1]
Panicum oligosanthes	n	n	n	-77[2]
Euphorbia corollata	n	-60[2]	n	-73[2]
Panicum leibergii	n	-66[2]	n	-100[2]
*Poa pratensis**	n	-77[2]	-81[2]	-100[2]

[a] No significant change.
*Based on frequency of occurrence.
[3] Significant at $P < .01$.
[1] Significant at $P < .10$.
[2] Significant at $P < .05$.

Fire Effects

The 10-year responses, percent change in mean number of individuals (frequency for sod-forming grasses), of individual species within each plot are presented in Table 3.

Species richness.

Species richness (total number) remained stable in all plots for the first eight years, fluctuating between 32 and 34 species. After the drought, richness dropped 25% on the plot burned in early spring and 30% on the plot burned in late spring. This suggests that negative synergistic effects resulted from the drought and spring burning.

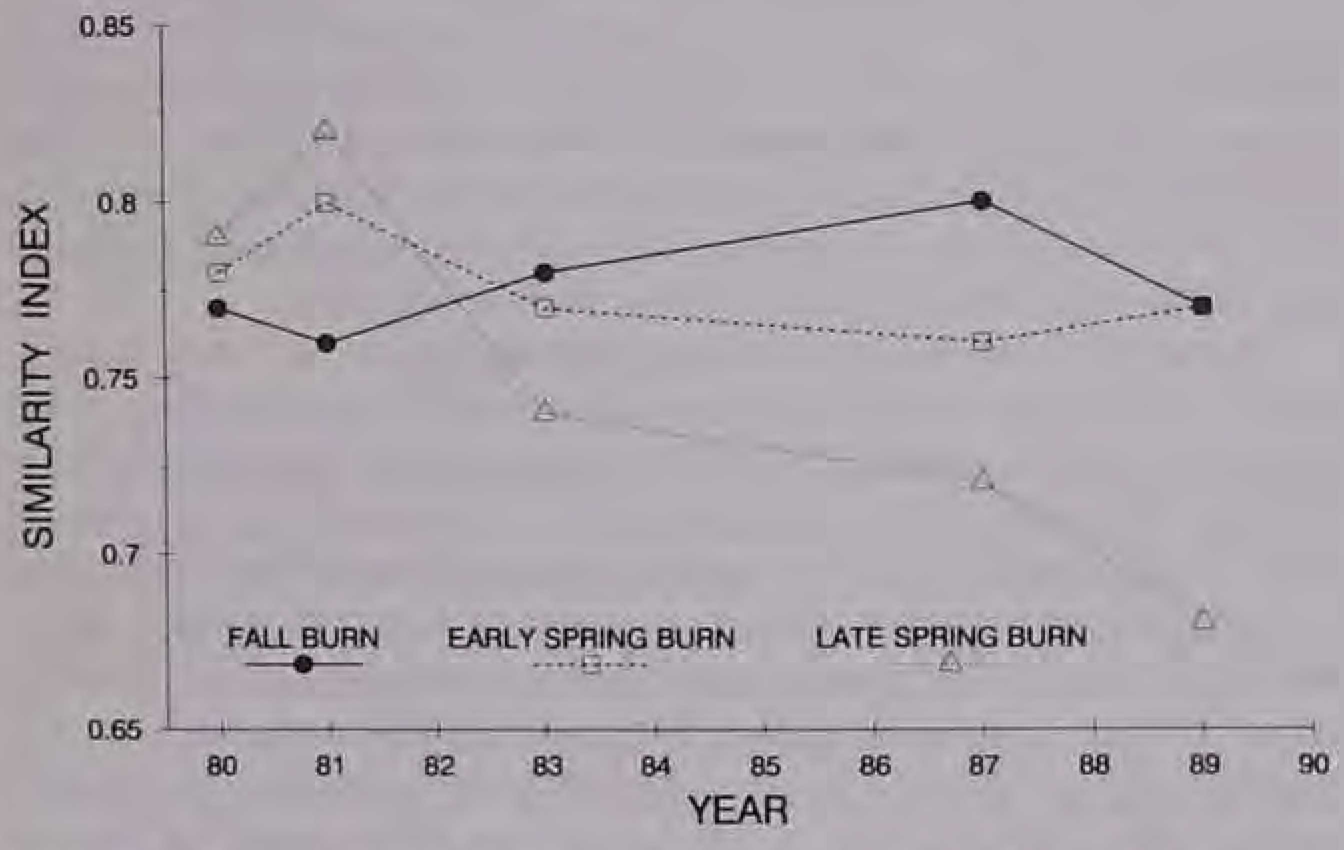

Figure 3. Similarity between burned plots and the unburned control over time. Index values are from a modified Sorensen's index of similarity after Curtis (1959) and Mueller-Dombois and Ellenberg (1974).

This decline in species richness on the spring burn plots was due mostly to the loss of rare species. Eight species with baseline frequencies of less than 10% prior to the drought were completely gone from the permanent quadrats one year after the drought.

These neutral to negative responses of species richness to fire are in contrast to other studies. Work by Weaver and Rowland (1952) and Anderson and Bailey (1980) suggests that burning eventually increases species richness in prairies. Possibly more time was needed for increases to become evident in this study, especially given that the study coincided with a severe drought.

Late spring burning.

Vegetation within the late spring burn plot changed markedly over the 10 years of the study, and in doing so, it diverged from the other test plots. The similarity indices between the late spring burn plot and the control declined (Figure 3), while they remained stable between the control and the other burn plots. This vegetation change in the late spring burn plot was due to declines in species density and diversity.

During the study, the late spring burn plot experienced a steady decline in species density. By the seventh year, it averaged 26% ($P < .0001$) fewer species per 0.25 m^2 than the other plots (Figure 1). Species diversity followed the same trend (Figure 2).

The reductions in species density and diversity are mostly attributable to declines in eight of the more common (baseline frequencies greater than 20%) species. These eight declining species fall into one of three categories as follows: 1) cool-season graminoids, Kentucky bluegrass, Leiberg's panic-grass, few-flowered panic-grass, and umbel sedge (*Carex umbellata* Schkuhr), 2) dense-crowned, bunch-grasses; prairie dropseed (*Sporobolus heterolepsis* Gray); and little bluestem (*Andropogon scoparius* Michx.), and 3) long-lived, summer-blooming forbs; flowering spurge (*Euphorbia corollata* L.); and showy sunflower (*Helianthus laetiflorus* Pers.).

The decline of the cool-season graminoids and the two bunchgrasses supports the findings of several studies (Towne and Owensby 1984, Svedarsky et al. 1986, Abrams and Hulbert 1987, Gibson and Hulbert 1987, Abrams 1988). The cause of cool-season plant decline under spring burning regimes has been generally attributed to 1) direct carbohydrate loss from lost foliage and 2) changes in microclimate that result in a less favorable environment (Henderson 1982, Hulbert 1988). Fire induced declines in warm-season bunchgrasses are often attributed to crown damage (Towne and Owensby 1984). Whether or not crown damage was a factor in this study is unknown.

Based on other studies (Gibson and Hulbert 1987, Towne and Owensby 1984), declines in some forbs were expected. However, it was a surprise that the forbs declining in this study were long-lived, summer-blooming species and not short-lived, spring-blooming species, such as prairie violet or blue-eyed grass. Prairie violet and blue-eyed grass numbers remained comparable between the late spring burn plot and the control, even though most of their seed production was lost 8 out of 10 years in the late spring plot.

Early spring burning.

Vegetation within the early spring burn plot remained similar to that of the unburned and late fall burn plots over the 10 years of the study. The similarity index between the unburned plot and the early spring burn plot remained stable (Figure 3), species density (mean number of species per 0.25 m^2) did not vary significantly among the early spring, late fall, and unburned plots (Figure 1), and the diversity indices remained similar among the early spring, late fall, and unburned plots (Figure 2).

Even though 10 years of early spring burning caused little change in the overall plant community, two forbs and three grasses did respond relative to the unburned plot. One forb, ground cherry, remained stable in the early spring burn plot, while its numbers in the unburned plot went down. The other, whorled milkweed

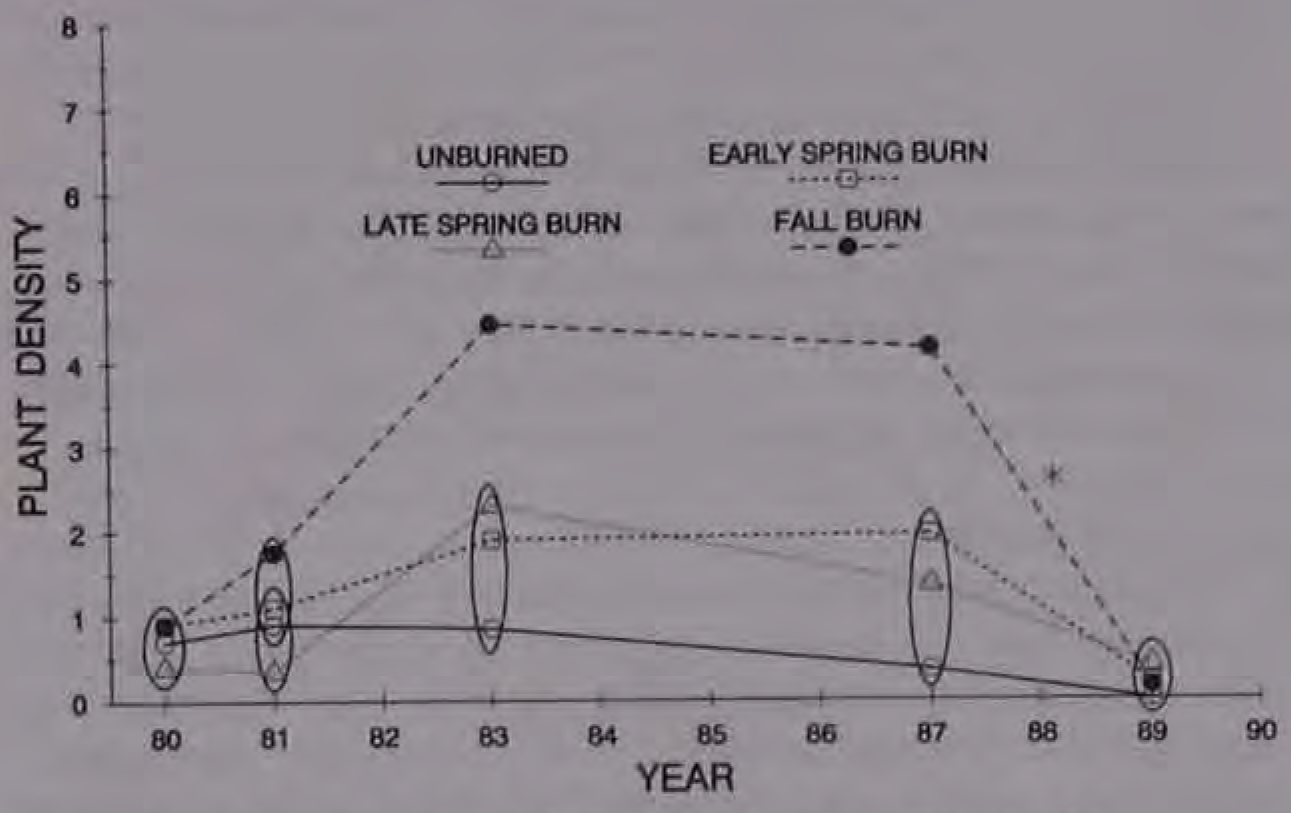

Figure 4. Mean number of blue-eyed grass (*Sisyrinchium campestre*) plants per 0.25 m^2 in response to seasonal timing of fire over time. Circled points are not significantly different from each other at the $P < .05$ level. An * indicates that the change over the 1988 drought is significant at the $P < .01$ level.

(*Asclepias verticillata* L.), remained stable in the early spring burn plot, while its numbers went up in the unburned plot. The general neutral response of forbs in the early spring burn plot of this study is in agreement with the Towne and Owensby (1984) study, where they found early spring burning in 48 out of 56 years caused little or no change in total perennial forb cover, exclusive of leadplant.

Among the grasses in this study, there was a classic cool-season vs. warm-season response in the early spring burn plot. Little bluestem, a warm-season grass, more than doubled its numbers, while Kentucky bluegrass, a cool-season grass, suffered an 80% decline in frequency. Long-term studies have clearly documented the positive effects of early spring burning, especially annual burning, on little bluestem (Towne and Owensby 1984, Svedarsky et al. 1986, Abrams and Hulbert 1987, Abrams 1988) and the negative effects of such fire regimes on Kentucky bluegrass (Nagel 1980, Towne and Owensby 1984, Svedarsky et al. 1986, Abrams and Hulbert 1987, Gibson and Hulbert 1987, Abrams 1988).

Late fall burning.

Vegetation within the late fall burn plot remained similar to that of the unburned and early spring burn plots over the 10 years of the study. The similarity index between the unburned plot and the late fall burn plot remained stable (Figure 3); species density (mean number of species per 0.25 m^2) did not vary significantly among the late fall, early spring, and unburned plots (Figure 1); and the diversity indices remained similar among the late fall, early spring, and unburned plots (Figure 2).

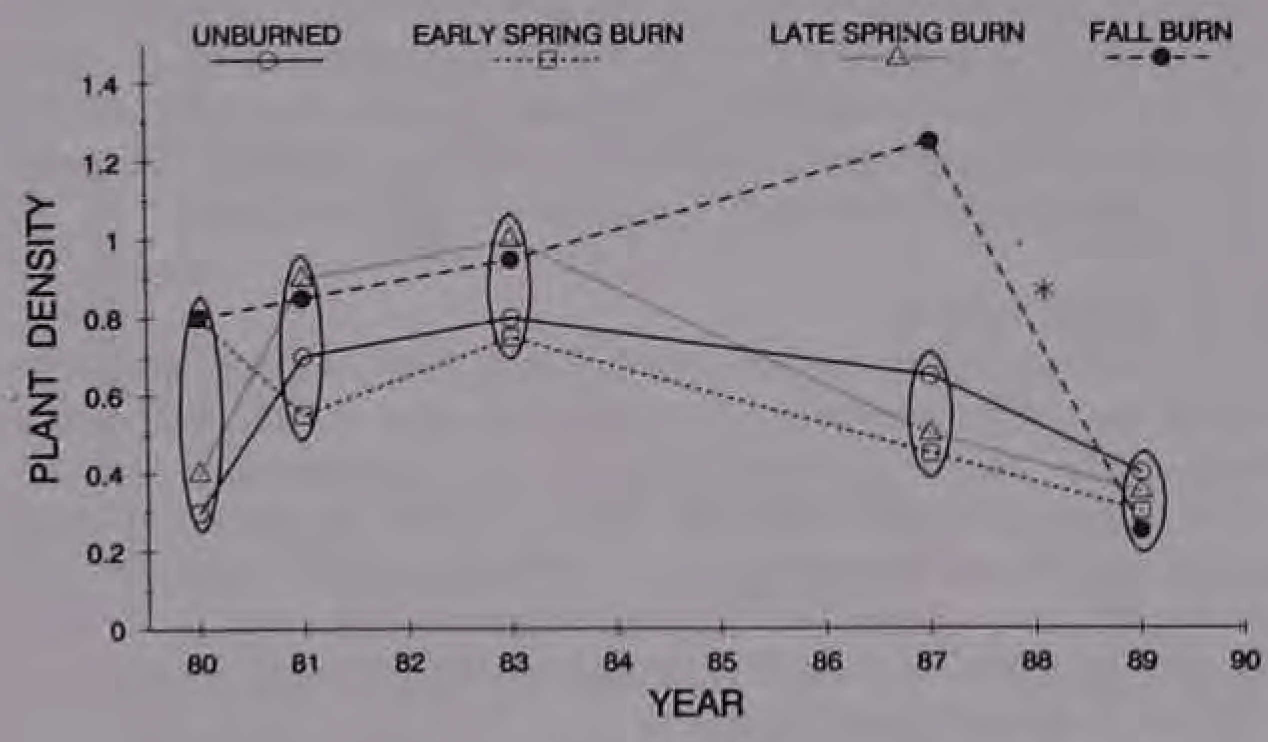

Figure 5. Mean number of prairie violet (*Viola pedatifida*) plants per 0.25 m^2 in response to seasonal timing of fire over time. Circled points are not significantly different from each other at the $P < .05$ level. An * indicates that the change over the 1988 drought is significant at the $P < .01$ level.

Within the late fall burn plot, as in the early spring burn plot, Kentucky bluegrass declined in frequency, and little bluestem increased in abundance. Towne and Owensby's (1984) 56 year study also found a negative response from Kentucky bluegrass (95% decline in cover) to fall burning. However, in contrast to this study, they also observed a negative response from little bluestem (20% decline in cover).

Of the nine forbs monitored in this study, four did not respond to the fall burning; two summer-blooming species, whorled milkweed and flowering spurge, responded negatively; and three spring- or fall-blooming species, blue-eyed grass, prairie violet, and sky-blue aster (*Aster azureus* Lindl.), appeared to benefit, at least up until the 1988 drought (Figures 4 and 5). In the Towne and Owensby (1984) study, they found total cover of perennial forbs, exclusive of leadplant, remained constant under late fall burning.

Indian grass and side-oats grama.

Indiangrass and side-oats grama, *Bouteloua curtipendula* (Michx.) showed no significant change in frequency during the course of this study. This is not surprising; both species were so abundant on the site that only dramatic declines would have been detected by frequency of occurrence data.

Big bluestem.

Big bluestem (*Andropogon gerardi* Vitman) showed no change in frequency during this study. This is in agreement with Konza Prairie studies (Abrams and Hulbert 1987, Gibson and Hulbert 1987, Abrams 1988), where no change in big bluestem frequency or cover were detected in 10 to 15 years of frequent burning. Given more time, however, big bluestem cover may eventually increase with frequent burning, as was found in the Towne and Owensby (1984) 56 year study. In degraded prairie, big bluestem's response to fire may be much faster. Svedarsky et al. (1986) reported annual spring burning of a degraded prairie increased big bluestem cover from 10% to 40% in just five years.

Needle-grass.

The positive response of needle-grass (*Stipa spartea* Trin.) to all burn treatments in this study (Table 3) was somewhat of a surprise. Because it is a cool-season species, a negative or at least neutral response was expected in the late spring, if not early spring, burn plots (Gibson and Hulbert 1987). However, others have also found needle-grass to benefit from fire. Anderson and Bailey (1980), working in a mid-grass prairie of Alberta, reported needle-grass frequency to be greater, but canopy cover to be less, on areas annually spring burned for 24 years compared to unburned areas. Svedarsky et al. (1986) reported needle-grass was favored by 13 years of annual spring burning in a degraded Minnesota prairie.

Improved seedling recruitment, and not better growing conditions, may be the primary benefit that needle-grass derives from fire. It is possible that thick mulch inhibits needle-grass seeds from drilling themselves into the ground. If this is the case, mulch removal by whatever means—even those resulting in less favorable growing environments—should eventually increase needle-grass numbers. This may explain the increased frequency, but reduced cover, found by Anderson and Bailey (1980), as well as the increase in density observed in the late spring burn plot of this study.

Leadplant.

The neutral response of leadplant (*Amorpha canescens* Pursh) to all burn treatments (Table 3) was unexpected. Other studies

(Towne and Owensby 1984, Abrams and Hulbert 1987) have reported generally favorable responses from leadplant to fire. It may be that the dryness of this study site hindered leadplant seedling establishment and, therefore, its ability to increase in response to fire. Evidence supporting this theory comes from observations of high leadplant seedling densities at the study site in 1990, following a period of ample rains. This level of seedling establishment was not seen at the site in the previous 10 years. Futher support for this recruitment theory comes from Abrams and Hulbert's (1987) study in which they found leadplant cover increased due to fire on mesic sites, but not on dry sites.

SUMMARY

Because this study was limited to one site, one must be cautious in trying to generalize its findings to other prairies. In addition, the lack of treatment replications within the site make it impossible to demonstrate conclusively that the burn treatments were responsible for the differences that developed between the plots over time. However, given the pre-treatment similarity of the plots, the long-term nature of the study, the consistent response trends that developed, and the general agreement of the results with other studies, it is highly likely that the treatments were responsible for most of the observed differences. But of course, replications of this or similar studies are needed on other prairies to confirm the responses observed here.

In summary, it appears that the 1988 drought and late spring burning were the only factors to cause significant changes in plant community composition. Of these two factors, drought seemed to be the most influential. The vegetation of the prairie seemed to change more from one year of severe drought than from 10 years of frequent early spring, late spring, or late fall burning. The drought coincided with sharp drops in species diversity and density (13% to 23%) across all plots. Shallow-rooted, early-blooming species—prairie violet, blue-eyed grass, panic-grasses, and Kentucky bluegrass—were hit the hardest. It also appeared that drought/fire interactions caused greater declines than the drought alone.

Of the treatments, late spring burning appeared to be the only one to cause a significant change in the prairie vegetation over the 10 years, resulting in declines of diversity and species density (30%). These shifts were due mostly to the loss of cool-season graminoids (Kentucky bluegrass, panic-grasses, and sedges), bunch-grasses (prairie dropseed and little bluestem), and some forbs (showy sunflower and flowering spurge), but *not* early-blooming forbs such as prairie violet and blue-eyed grass.

Other notable species responses included a strong positive response from needle-grass (4- to 20-fold increase in density) in all burn treatments, while remaining stable in the unburned plot. It was speculated that litter removal by the fires resulted in greater seedling establishment by needle-grass. Also, there were some indications that late fall burning was beneficial to some cool-season forbs (prairie violet, blue-eyed grass, and sky-blue aster), at least in the absence of spring/summer drought.

ACKNOWLEDGEMENTS

The first three years of this study were supported in part by a grant from the University of Wisconsin-Madison HATCH fund. I thank David Lovell for data collected in 1981, 1982, and 1983. I thank Paul Rasmussen for statistical review, Jerry Bartelt and Lisa Hartman for editorial review, and Brian Dhuey for computer graphics. I also acknowledge the field assistance of Karen Agee, Amy Parkinson, and others who helped over the years. Lastly, I thank the Miller family for their generosity in allowing this study to be conducted on their prairie.

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ALIEN SPECIES COVER ON THE PERIMETER OF TWO NORTHWEST IOWA PRAIRIES

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Abstract. Perimeters of two northwest Iowa prairies were sampled with 20, 20 x 50 cm quadrats placed at 1 m intervals along six transects laid perpendicular to the edge of each prairie. Within each quadrat, cover was estimated for alien and native prairie species, and linear regression of percent alien cover was calculated for each transect. Mean distance inward from the prairie edge where the regression line indicated alien species cover would become zero was 22.8 m with a range from 16.2 m to 28.0 m. One prairie showed significantly narrower perimeter belts in lowland (mean 16.3 m) than in upland (mean 22.2 m) sites. Assuming a perimeter belt of 22.8 m, prairies less than 0.2 ha would not be expected to have any areas free of alien species. Because of greater cover by exotic species, differential management of prairie perimeters might be necessary.

INTRODUCTION

In Iowa, almost all prairie remnants are surrounded by stands of alien species. At the interface, the invasive dynamics of the two floras, under the constraints of environmental conditions, determines the extent of intermingling of prairie and alien vegetation. Usually, the alien species are being actively managed in agricultural or roadside situations, in a way that often has detrimental effects on adjacent prairie. Drift of herbicides and surface runoff of pesticides and fertilizer impact the prairie vegetation and allow more tolerant exotic species to invade into prairie.

Even in prairie areas of high quality, several alien species will likely be found throughout the entire area. Principal among these is Kentucky bluegrass (*Poa pratensis* L.) (Weaver 1968). Hardly a square meter of prairie in Iowa is not infested with at least one alien species.

The extent of the invasion and degradation of prairie by alien species has great implications both for minimum viable size and for management of prairies. If a prairie remnant is sufficiently small, here may be no part of it free of alien species. There also may be some minimum size, below which preservation is not feasible because the impact of surrounding alien vegetation dominates the prairie component of the vegetation. If the perimeter of a prairie has a component of alien species, it may be necessary to manage the perimeter differently to discourage aliens and encourage prairie species.

For these reasons, it is important to know the probable size of he invasion zone in prairies of different types and in different locations.

In order to asses the extent of invasion by alien species, I estimated and analyzed alien species cover in the perimeter belts of two northwest Iowa prairies.

METHODS

Two state-owned prairies in Iowa were studied. Cayler Prairie (Aikman and Thorne 1956) is a 64.7-ha (160-A) tallgrass prairie ocated in Dickinson County (T-99, R-37, S-17) (Roosa 1981). The prairie has been owned by the State of Iowa since 1960 and is managed, principally by spring burning, by the Iowa Department of Natural Resources. It is bordered by pasture on its north and east sides, county road on the west, and Conservation Reserve land and lfalfa hayland on the south. Transects were laid out on the west and south sides.

Anderson Prairie, also known as Emmet County Prairie (Roosa 1981), is a 80.9-ha (200-A) tallgrass prairie located in Emmet County (T-100, R-34, S-33) (Roosa 1981). The prairie was purchased by the State of Iowa in 1980 and is managed, principally by spring burning, by the Emmet County Conservation Board. The west 16.2-ha (40-A) portion of the prairie was chosen for this study. Transects were placed on the west side, bordered by a county road, and on the south side, bordered by pasture.

In each prairie, six 20-m transects were laid out perpendicular to the boundary, four in upland and two in lowland sites. After stratification into upland and lowland types, representative sites were chosen by inspection. Field work was conducted in early July 1989.

Twenty 20 x 50 cm quadrats were placed at 1-m intervals along each transect with the long edge of the quadrat perpendicular to the transect. Within quadrats, cover of each species was estimated by cover class according to a method used by Daubenmire (1959). Total alien cover and total prairie cover was estimated by summing the cover of component species. Percent alien cover and percent prairie cover were then determined

Linear regression of the percent alien cover was calculated, and the point at which the regression line crossed the ordinate (x) axis was determined. That point is termed the extinction point for alien species cover.

RESULTS

The mean distance to the extinction point for all transects was 22.7 m with no statistical difference (p=.05) between the two prairies. Only at Anderson Prairie was there a statistical difference between upland and lowland extinction points (p=<.01) (Table 1).

Linear regression plots graphically show little difference between upland and lowland transects for Cayler Prairie (Figure 1)

Table 1. Extinction point of alien species cover (m).

	Cayler Prairie	*Anderson Prairie*
	Lowland transects	
	23.4	16.2
	22.1	16.4
Mean (SD)	22.7 (0.9)	16.3** (0.1)
	Upland transects	
	28.8	26.0
	17.9	24.3
	23.4	27.7
	18.6	28.3
Mean (SD)	22.1 (5.0)	26.6** (1.8)
	Both upland and lowland transects	
Mean (SD)	22.4 (3.9)	23.1 (5.5)

** Significant difference at P=.01.

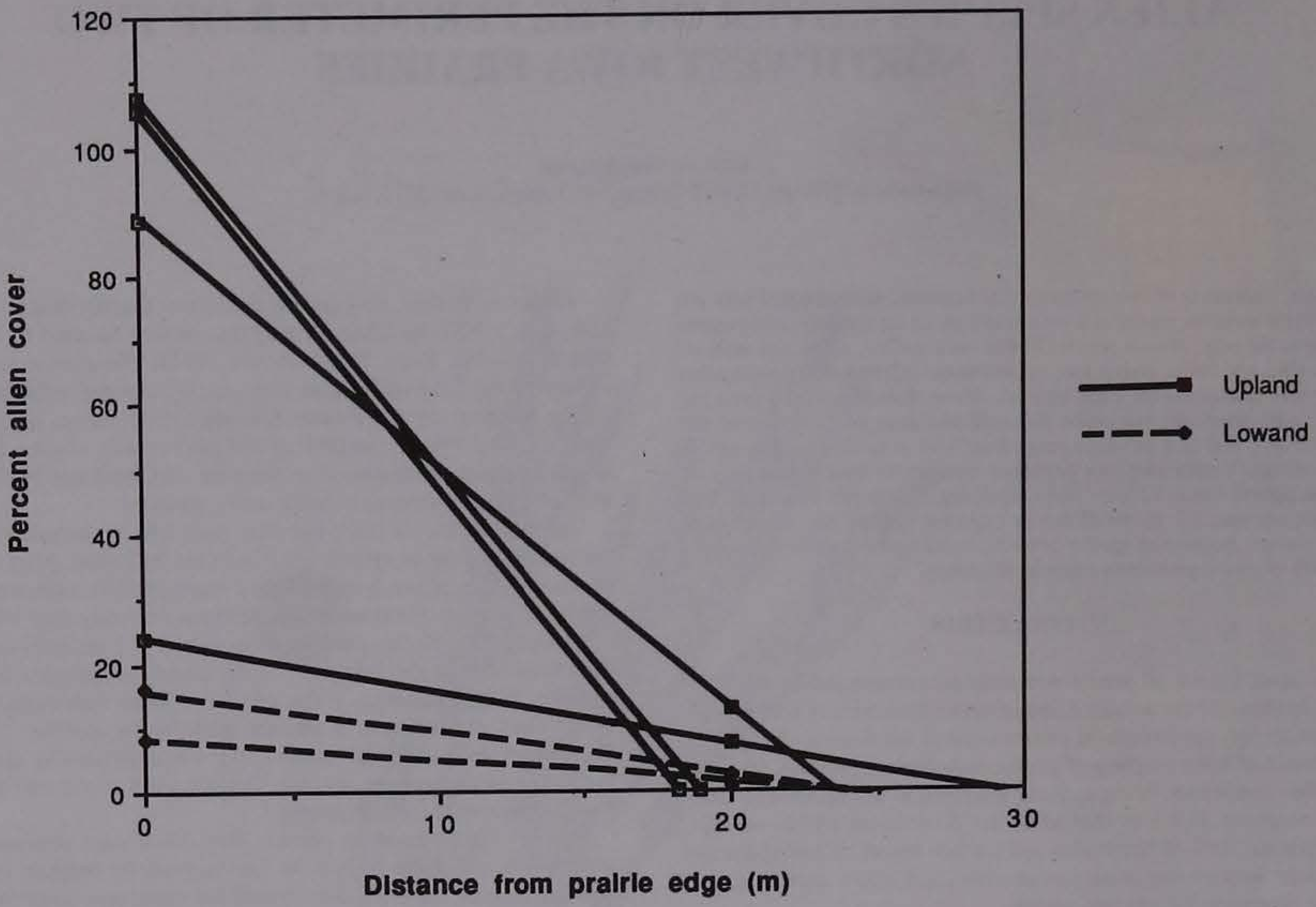

Figure 1. Linear regression of percent alien cover on distance from prairie edge for Cayler Prairie.

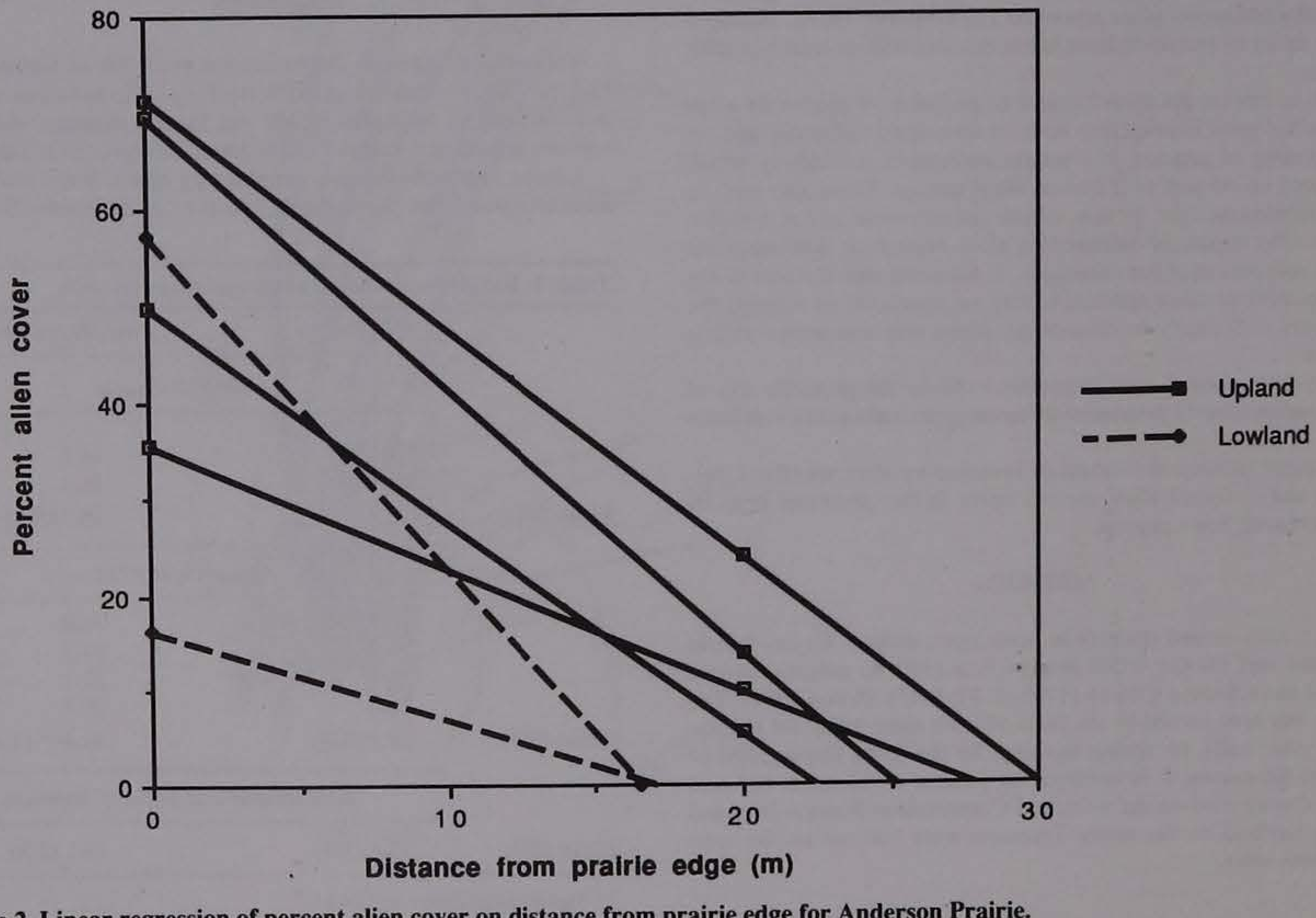

Figure 2. Linear regression of percent alien cover on distance from prairie edge for Anderson Prairie.

while there is evident difference between upland and lowland sites at Anderson Prairie (Figure 2). In both prairies, the alien cover was generally lower in the lowland sites. Alien cover consisted mainly of smooth bromegrass (*Bromus inermis* Leysser) and Kentucky bluegrass.

DISCUSSION

An appreciable portion of each prairie contained alien vegetation. On Cayler Prairie, with a mean alien perimeter belt of 22.4 m, a total of 7.0 ha would be involved, 10.8% of the 64.7-ha prairie. At Anderson Prairie, the alien perimeter belt was slightly wider, at 23.2 m. Of the 16.2-ha portion studied, 21.7% would be expected to be contaminated with alien species.

Although there were differences between vegetation adjacent to the prairie sites, the extent and type of alien invasion on the 12 transects did not show any consistent pattern with the adjacent vegetation type.

In this study, lowland sites had lower levels of invasion by aliens than upland sites. Figures 1 and 2 show that percent cover of aliens at the prairie edge was lower for lowland sites in three of four transects. Observations of the sites indicated prairie communities dominated by species such as big-tooth sunflower (*Helianthus grossesserratus* Martens) resisted invasion more successfully than upland communities dominated by big bluestem (*Andropogon gerardii* Vitman).

These perimeter belts represent a significant portion of each prairie. When management is being considered, it might be useful to treat the perimeter as a region requiring special consideration to maximize negative impact on invaders while enhancing cover of prairie species.

When considering minimum prairie size for preservation, the portion of the prairie containing alien species should be taken into account. Assuming a perimeter belt of 22.4 m containing alien species, a rectangular site 44.7 m on each side (0.2 ha) wouldn't be expected to have any area free of alien invasion.

ACKNOWLEDGEMENTS

I wish to recognize the Iowa Preserves Advisory Board for permission to carry out this research project on the two state preserves. I also wish to acknowledge the cooperation of Iowa Lakeside Laboratory for use of their laboratory and housing facilities during the project.

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LOESS HILLS PRAIRIES AS BUTTERFLY SURVIVIA: OPPORTUNITIES AND CHALLENGES

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Abstract. The Loess Hills landform contains the largest remaining tracts of prairie in Iowa. Prairie-restricted butterfly species are among the last surviving native fauna found on these scattered tracts. Surveys of the historical and present distribution of these species show a continued decline in the number of species and populations. A few parks and preserves function as refugia for these widely separated populations. These prairies are really "survivia" for these and other invertebrate species because, although populations survive here, they are threatened by various forms of disturbance, including continued loss of prairie to agriculture, development, leafy spurge infestation, and woodland succession. For populations in parks and preserves, the effects of prairie vegetation management techniques, such as fire, are still unclear but are potentially damaging. The Loess Hills landform prairies present unique opportunities for studying these relationships and unique challenges for managing these populations.

INTRODUCTION

The Loess Hills landform parallels the course of the Missouri River, beginning in the north at Union County, South Dakota, running southward most of the length of Iowa's western border, and ending in Holt and Atchison counties in northwestern Missouri. The hills are formed of fine-grained particles of silt from the Missouri River bottomlands blown eastward by prevailing winds. While loess mantling is a common occurrence, the depth and breadth of the deposits here are, on a global scale, nearly unique (Prior 1976). These deposits, reaching over 200 feet deep and fifteen miles wide in various places, constitute a landform. Erosion after deposition turned these deposits into steep, highly dissected ridges and narrow, deeply eroded valleys. This abrupt relief and the dry, windblown microclimate made these prairies less desirable for cultivation than were the blacksoil, tallgrass prairies to the east and immediately to the west. The Loess Hills landform contains the largest remaining tracts of prairie in Iowa.

The Loess Hills are in a transition zone where either woodland or prairie can grow. In a comprehensive floristic study, Novacek et al. (1985) noted that some of the westernmost remnants of eastern deciduous forest extend as a peninsula northward and westward from Missouri up the Loess Hills, decreasing in species diversity northward. These remnants are largest on the less-exposed north- and east-facing slopes of the hills. On the drier, hotter, west- and south-facing slopes, the plant and animal communities share affinities to mixed-grass prairie communities of the Great Plains to the west. These Great Plains species include buffalo berry, *Shepherdia argentea* (Pursh) Nutt; nine-anther dalea, *Dalea enneandra* Nutt.; skelton weed, *Lygodesmia juncea* (Pursh) Hook; scarlet gaura, *Gaura coccinea* Pursh; western prairie clover, *Petalostemum occidentale* (Gray) Fern.; cowboy's delight, *Sphaeralcea coccinea* (Pursh) Rydb.; and yucca, *Yucca glauca* Nutt. Novacek (1985) noted that the dominant grass species included little bluestem, *Andropogon scoparius* Michx., and side-oats grama, *Bouteloua curtipendula* (Michx.) Torr. Novacek et al. (1985) listed 17 western species that reach the easternmost extent of their range in the Loess Hills. They propose a south-easterly migrational route for these species along the Missouri River corridor. A peninsular prairie gradient, inverse of the woodland gradient, also exists from north to south, as prairie species diversity decreases southward. However, some southern Great Plains species are found only in the southernmost Loess Hills. Some of these same abundance distribution patterns seem to hold for Loess Hills butterflies.

Since most of the larger grazers and carnivores and some bird species have been extirpated from the Loess Hills, invertebrate species are among the last surviving prairie-restricted fauna on these scattered tracts. Butterfly species are merely the best-known and best-documented of the invertebrates; they may be indicators of the status of thousands of other species for which we have little or no documentation. While some butterfly species are quite adaptable to disturbance or habitat destruction, others are tied to certain plant species which they require for uses including larval host-plants, perching sites, or egg-laying sites. These butterfly species disappear when the key plant species are eliminated through habitat destruction.

John Downey has suggested that prairie remnants, which are sometimes thought of as refugia for these species, might better be called "survivia" (Downey and Schlicht, unpublished). These Loess Hills prairie sites are still rich in prairie-restricted fauna, but they have a settlement history that is relatively recent. While populations continue to exist on some of these scattered sites, their long-term viability is questionable. Wilcove (1987) described the pattern of species loss characteristic of such fragmented ecosystems. Several species of butterflies may have already disappeared from these prairies, due to the destruction of prairie habitats.

In the Loess Hills, as in many prairie remnant environments, opportunities exist to preserve plant-invertebrate communities. Because, by sheer number of species, invertebrates are the dominant life form on these prairies, managers should consider them when they manage prairies. Current prairie management techniques often focus solely on managing these remnants for botanical elements. While these practices lead to handsome prairies, little is known about the effect of these practices on fauna such as prairie invertebrates. While many invertebrate species will be unaffected by management practices, a significant number of these species could be adversely affected. Managing these prairie survivia in a way that will also preserve prairie-restricted invertebrates presents many challenges.

METHODS

Baseline data for this project were kindly provided by Dennis Schlicht of the Iowa Lepidoptera Project. The Iowa Lepidoptera Project maintains the largest collection of Iowa butterfly specimens extant. J. C. Downey and Schlicht have also compiled all known records of Iowa butterfly sightings. These records include a complete search of literature prior to 1988; extensive searches of museum records, including all known from Iowa colleges; and compilation of the yearly updates published as the *Season Summaries* of the Lepidopterists' Society and 4th of July Butterfly Counts of the Xerces Society. Also housed at the Project are many unpublished records, including extensive records compiled in the last ten years by Cuthrell, Downey, Fleckenstein, Harms, Nekola, Schlicht, Selby, and Orwig. Researchers interested in accessing these records can contact the Iowa Lepidoptera Project in care of Schlicht, 1108 1st Ave., Center Point, Iowa 52213.

Of particular importance to this study and other studies of the Loess Hills are the records by Lindsey (1921) and Lindsey et al. (1931), which provide an extensive baseline for Woodbury County, and the unpublished records of the Loess Hills Skipper Foray of

1980, coordinated by Downey and conducted by a number of lepidop-terists from around the nation.

I conducted surveys for this paper over a six-year period, from 1985 to 1990. A total of 49 sites throughout the Iowa Loess Hills were visited. Surveys were conducted on 128 dates, ranging throughout the season, from March 26 to October 26. Identification of specimens to the species level was confirmed by Schlict. Most records are represented by voucher specimens in my possession or deposited with the Iowa Lepidoptera Project.

Nomenclature for plant species follows Great Plains Flora Association (1986). Nomenclature for butterfly species in this paper follows Ferris (1989).

RESULTS

Ninety-nine species of butterflies, including two separate subspecies, have been recorded from Loess Hills counties; more than one fourth are habitat restricted (Table 1). My inventories of Sioux City Prairie, a 61-ha tract in Sioux City, have yielded 56 species, a dozen of which are habitat restricted. Of the 37 species of butterflies that have been recorded as being present in all the Loess Hills counties of Iowa, the regal fritillary, *Speyeria idalia* (Drury), and four others are habitat restricted.

Surveys of the historical and present distribution of habitat-restricted butterfly species show a continued decline in the number of species and populations. Table 2 shows eight butterfly species which have been known and previously collected from Woodbury County, Iowa, but have not been reported or collected since 1922 and are apparently extirpated. Woodbury is the only Loess Hills county for which we have extensive early records. The Dakota skipper, *Hesperia dacotae* (Skinner), and the Powesheik skipper, *Oarisma powesheik* (Parker), seem to be especially sensitive to disturbance (Dana and Huber 1988). Recent sightings of these once wide-ranging northern prairie skippers are limited in Iowa to prairies in the north-central part of the state. The last known Iowa population of the state-endangered Dakota skipper, at Cayler Prairie in Dickinson County, appears to have been extirpated in the 1980s.

The regal fritillary, a common Loess Hills butterfly and largest of the prairie species, is becoming progressively rarer in eastern meadows and prairie preserves (Scott 1986). The larvae feed on wild violet, *Viola* spp. Opler and Krizek (1984) noted that the regal fritillary has almost disappeared from the Maritime Provinces and New England and has "declined precipitously" elsewhere. This is particularly disquieting because the regal is a strong flier and a rapid disperser, seemingly well-suited to adapting to disturbance and recolonizing after burns. Ferge (1990) argued that it is declining because of the loss of large contiguous prairie tracts supporting a diverse group of nectar sources and the vulnerability of overwintering larvae to fire management.

The olympia marblewing, *Euchloe olympia* W.H. Edwards, a woodland edge-savannah species, is common on a few of the steepest loess bluffs. It flies only for a month in spring. It is rarely found elsewhere in the state, and several of the Loess Hills county records are of single individuals.

The dusted skipper, *Atrytonopsis hianna hianna* (Scudder), is also a spring prairie flier. Only one Iowa county outside the Loess Hills is known to contain populations. The larvae feed exclusively on big bluestem, *Andropogon gerardii* Vitman, or little bluestem.

The dry-prairie ottoe skipper, *Hesperia ottoe* W.H. Edwards, is thought to be more abundant in the northern Loess Hills than anywhere else in its range (Dana and Huber 1988). Only three other widely scattered Iowa counties outside the Loess Hills are currently known to contain populations. Adults fly in early summer and perch and lay eggs on coneflowers, *Echinacea* spp., or the larval hostplants, several prairie grasses.

The blazingstar skipper, which flies only in the fall, is a prime illustration of the unique nature of the Loess Hills. Two quite distinct subspecies, once thought separate species, are found in the Loess Hills but have not been collected recently from the rest of the state. *Hesperia leonardus pawnee* Dodge is a Great Plains skipper whose larvae feed mostly on short grasses, such as little bluestem. The larvae of *Hesperia leonardus leonardus* Harris feed on switchgrass, *Panicum virgatum* L., or bluestems in eastern woodland meadows or clearings. The two subspecies appear to be intermingling in the central Loess Hills, as specimens there intergrade in wing characteristics.

Several woodland or savannah-restricted species occur in western Iowa only in the southern Loess Hills: the sleepy duskywing, *Erynnis brizo brizo* (Boisduval and Le Conte); the zebra swallowtail, *Eurytides marcellus* (Cramer); the hickory hairstreak, *Satyrium caryaevorum* (McDunnough); the white-M hairstreak, *Parrhasius m-album* (Boisduval and Le Conte); and Henry's elfin, *Incisalia henrici henrici* (Grote and Robinson). Northern prairie or Great Plains species found only as far south as Pottawattamie County include the Iowa skipper, *Atrytone arogos iowa* (Scudder); the orange-bordered blue, *Lycaeides melissa melissa* (W.H. Edwards); and the Aphrodite, *Speyeria aphrodite alcestis* (W.H. Edwards). The orange-bordered blue appears to be expanding southward through the hills.

DISCUSSION

The Loess Hills landform presents many opportunities for preservation and study of prairies. The prairies remaining there are among the largest in the state and represent the largest number of remnant sites. Many of the sites are still of high quality, and they contain a high biodiversity of plants and animals. They represent a globally unique community, and a number of areas have already been preserved by landowners, prairie enthusiasts, county conservation boards, private foundations, the Iowa Department of Natural Resources, and The Nature Conservancy.

But these prairies also present significant challenges. More preserves need to be acquired, and current preserves need to be monitored, enlarged, and buffered. Sioux City Prairie, for example, is threatened by expansion of an adjacent college. An already thin buffer strip of good-quality prairie was bulldozed in the spring of 1991. Less enlightened institutions continue to destroy remnant prairie throughout the length of the Loess Hills. Loss of habitat has caused the greatest loss of butterfly species and populations in the Loess Hills and will continue to be the greatest threat to remaining unprotected prairies.

Once sites are acquired, management responsibilities are enormous. Already overburdened area managers are often asked to manage nearby, new prairie acquisitions with no additional staff. None of the sites has yet been surveyed for a comprehensive inventory of all the biological components. Further, complicated questions need to be answered: Should these sites be managed as prairies or forests in the places where the two habitats coexist on opposite sides of the hill? Should some sites be managed as savannas? Since most sites are currently unmanaged or have been managed for less than ten years, management decisions made now will shape the future of each of these sites.

The management tool of choice on these prairies is currently fire. Reasons given for this are the ability to control invasive cool-season grasses, trees, and brush; labor shortages; and time constraints. Most fire management is done during a window of a few weeks each spring, and it may be postponed because of spring showers or windy days. If the manager is unable to burn within that window, then the prairie will stay unburned for that year. Although fire certainly was a part of Loess Hills history and a natural maintenance agent for these prairies, many changes occurred on these prairies with the arrival of the pioneers: fragmentation, removal of large grazers, changes in fire intervals, invasion of exotic species. The effect of fire on these prairies has changed as the prairies have changed.

Table 1. Butterfly species recorded from the Loess Hills counties in Iowa (Plymouth, Woodbury, Monona, Harrison, Pottawattamie, Mills, and Fremont) through 1990.

Species	*Habitat-restricted species*	*Number of counties*
Hesperioidea		
Epargyreus clarus clarus (Cramer)		7
Achalarus lyciades (Geyer)		1
Thorybes bathyllus (J. E. Smith)		6
Thorybes pylades (Scudder)		7
Staphylus hayhurstii (W. H. Edwards)		4
Erynnis brizo brizo (Boisduval and Le Conte)	x	2
Erynnis juvenalis juvenalis (Fabricius)		5
Erynnis horatius (Scudder and Burgess)	x	5
Erynnis martialis (Scudder)	x	6
Erynnis baptisiae (Forbes)	x	2
Erynnis persius persius (Scudder)	x	1
Pyrgus communis (Grote)		7
Pholisora catullus (Fabricius)		7
Ancyloxypha numitor (Fabricius)		3
Oarisma powesheik (Parker)	x	1
Hylephila phyleus phyleus (Drury)		1
Hesperia ottoe W. H. Edwards	x	7
Hesperia leonardus leonardus Harris	x	5
Hesperia leonardus pawnee Dodge	x	6
Hesperia dacotae (Skinner)	x	1
Polites peckius (W. Kirby)		6
Polites themistocles (Latreille)		7
Polites origenes origenes (Fabricius)	x	6
Polites mystic dacotah (W. H. Edwards)	x	3
Wallengrenia egeremet (Scudder)		3
Pompeius verna (W. H. Edwards)		6
Atalopedes campestris huron (W. H. Edwards)		5
Atrytone arogos iowa (Scudder)	x	3
Atrytone logan logan (W. H. Edwards)		7
Poanes hobomok hobomok (Harris)		6
Euphyes dion (W. H. Edwards)	x	1
Euphyes bimacula illinois (Dodge)		1
Euphyes vestris metacomet (Harris)		6
Atrytonopsis hianna hianna (Scudder)	x	7
Amblyscirtes vialis (W. H. Edwards)		7
Lerodea eufala (W. H. Edwards)		2
Papilionidae		
Eurytides marcellus (Cramer)	x	1
Papilio polyxenes asterius Stoll		7
Heraclides cresphontes (Cramer)		7
Pterourus glaucus glaucus (Linnaeus)		7
Pterourus troilus troilus (Linnaeus)		1
Pieridae		
Pontia protodice (Boisduval and Le Conte)		6
Pieris rapae (Linnaeus)		7
Euchloe olympia W. H. Edwards	x	7
Colias philodice philodice Godart		7
Colias eurytheme Boisduval		7
Zerene cesonia cesonia (Stoll)		7
Phoebis sennae eubele (Linnaeus)		5
Eurema lisa lisa (Boisduval and Le Conte)		5
Eurema nicippe (Cramer)		2
Nathalis iole Boisduval		3
Lycaenidae		
Feniseca tarquinius tarquinius (Fabricius)		2
Gaeides xanthoides dione (Scudder)		7
Hyllolycaena hyllus (Cramer)		6
Harkenclenus titus titus (Fabricius)		7
Satyrium acadicum acadicum (W. H. Edwards)	x	3
Satyrium edwardsii (Grote and Robinson)	x	2
Satyrium calanus falacer (Godart)		7
Satyrium caryaevorum (McDunnough)	x	3
Satyrium liparops strigosum (Harris)	x	4
Mitoura grynea grynea (Hubner)	x	6
Incisalia henrici henrici (Grote and Robinson)	x	3
Parrhasius m-album (Boisduval and Le Conte)	x	1
Strymon melinus humuli (Harris)		6
Leptotes marina (Reakirt)		1
Hemiargus isola alce (W. H. Edwards)		7
Everes comyntas comyntas (Godart)		7
Celastrina argiolus ladon (Cramer)		7
Lycaeides melissa melissa (W. H. Edwards)		5
Plebejus saepiolus amica (W. H. Edwards)		1
Libytheidae		
Libytheana bachmanii bachmanii (Kirtland)		2
Nymphalidae		
Euptoieta claudia (Cramer)		4
Speyeria cybele cybele (Fabricius)		7
Speyeria aphrodite alcestis (W. H. Edwards)	x	4
Speyeria idalia (Drury)	x	7
Clossiana selene myrina (Cramer)	x	1
Clossiana bellona bellona (Fabricius)		1
Charidryas gorgone carlota (Reakirt)		7
Charidryas nycteis nycteis (Doubleday and Hewitson)		6
Phyciodes tharos tharos (Drury)		7
Phyciodes batesii (Reakirt)		1
Polygonia interrogationis (Fabricius)		7
Polygonia comma (Harris)		6
Polygonia progne progne (Cramer)		5
Nymphalis antiopa antiopa (Linnaeus)		7
Aglais milberti milberti (Godart)		1
Vanessa virginiensis (Drury)		4
Vanessa cardui (Drury)		7
Vanessa atalanta rubria (Fruhstorfer)		7
Junonia coenia Hubner		3
Basilarchia arthemis astyanax (Fabricius)		7
Basilarchia archippus archippus (Cramer)		6
Mestra amymone (Menetries)		1
Anaea andria Scudder		1
Asterocampa celtis celtis (Boisduval and Le Conte)		7
Asterocampa clyton clyton (Boisduval and Le Conte)		5
Satyridae		
Enodia anthedon A. H. Clark	x	4
Megisto cymela cymela (Cramer)		7
Cercyonis pegala olympus (W. H. Edwards)		7
Danaidae		
Danaus plexippus (Linnaeus)		7

Table 2. Butterfly species currently presumed extirpated from Woodbury County, Iowa.

Species		*Habitat*	*Latest record*
Common name	*Latin name*		
Powesheik skipper	*Oarisma powesheik* (Parker)	prairie	1917
Dakota skipper	*Hesperia dacotae* (Skinner)	prairie	1922
Two-spotted skipper	*Euphyes bimacula illinois* (Dodge)	wetland	1917
Acadian hairstreak	*Satyrium acadicum acadicum* (W. H. Edwards)	prairie	1922
Edwards' hairstreak	*Satyrium edwardsii* (Grote and Robinson)	oak thickets	1917
Aphrodite	*Speyeria aphrodite alcestis* (W. H. Edwards)	prairie	1917
Silver bordered fritillary	*Clossiana selene myrina* (Cramer)	wetland	1915
Meadow fritillary	*Clossiana bellona bellona* (Fabricius)	prairie/meadow	1915

Schweitzer (1985) noted that the rare elements of these prairies, the regal fritillary and the prairie skippers, along with *Papaipema* spp. moths, could be very sensitive to fire. Panzer (1988) advocated burning with restraint and recommends mowing in some instances. (Nekola 1990) suggested that misdirected management may cause a greater loss of biodiversity in a site than no management at all. Thomas (1984) showed how well-intentioned preservation of the habitats of the pastureland large blue, *Maculinea arion* L., in Britain caused its extirpation. Sheep were removed from the sites, and grasses were allowed to grow up. This caused the soil temperature to drop and brought about the extirpation on the sites of an ant species which the large blue larvae relied upon in a mutualistic relationship. This complex relationship was unknown to the managers until it was too late. The irreversibility of most extirpation should cause managers to examine these questions carefully.

These prairie remnants are no longer an intact ecosystem, so fire now will have different effects for several reasons. The fragmentation of prairies into islands impedes the old mechanisms of recolonization after a burn. Panzer (1988) found Culver's root, *Veronicastrum virginicum* (L.) Farw., and borer moths, *Silphium* spp., were confined to a 1-ha section of a 70-ha prairie in Illinois. If the population is sensitive to fire and this patch is burned, then the population will be extirpated from that prairie. If the next prairie is now at the other end of the county instead of over the next rise, the site will not be recolonized. Many current prairies may already be too small to support viable populations of some species. A recent study of the Karner blue, *Lycaeides melissa samuelis* Nabokov, recommended at least 810 ha for a viable preserve, given a very careful management regime (Givnish et al. 1988).

The removal of large grazers also breaks another link in the chain of the ecosystem. Large grazers had major effects on the prairie. Larson and Murdock (1989) noted that a herd of bison grazed a prairie intensely, created wallows and trails, and then moved on, leaving a very dissected grassland when fire came through. The resulting burns were patchy, and many small areas remained as recolonization sources, even in a large fire. Current practices of lighting some skips should be discouraged. Bison also slowed woody invasion by rubbing down trees on the prairie edge, and by heavily grazing young sumac, *Rhus* spp., shoots in spring.

Another change comes in the frequency of burn intervals. Wendtland and Dodd (1990) researched historic burn intervals at Scotts Bluff National Monument and found that the maximum frequency of wildfire return for any one site was thirteen years. Fire frequency overall averaged 20-30 years. Current fire management plans in the Loess Hills call for burn intervals of one in five years to two in three years. While badly degraded areas may need this frequency initially, it seems severe as a standard for high-quality sites.

Further questions should be asked about the burn window itself. Wentland and Dodd (1990) suggested that presettlement fires were large and occurred most often in late summer. After settlement, fires occurred most often in spring. While all prairie species must have some adaptation to fire, that adaptation could be negated by this switch in the burn window.

The greatest potential difficulty may be the introduction of exotics such as leafy spurge, *Euphorbia esula* L. Nearly impossible to eradicate, this plant thrives and expands under a program of burn management. It has already crept into several preserves in the northern Loess Hills.

To promote biodiversity, we must consider diversified styles of management. Sioux City Prairie, owned by The Nature Conservancy (TNC), is a good example of a site with diverse management provided by TNC, the Woodbury County Conservation Board, and a group of dedicated volunteers led by Bill and Dianne Blankenship. While the traditional burn pattern is followed, it is curtailed in drought years, and fall burns have varied the burn window. Sumac stands were cut by hand, and the stumps were treated with spot application of herbicide. Some established invasive trees were girdled, and others were cut and removed. Volunteers controlled invasive thistles by removing seed heads by hand and bagging them. Volunteers also wick-applied herbicide to any leafy spurge plants found on the prairie. These techniques, while labor intensive, have also served to get more people interested in prairie, and caused them to value it more highly.

These practices go a long way towards fostering biodiversity. Other practices can also help preserve prairie invertebrates. Managers should survey invertebrate populations in as great a detail as possible. Burn units should be designed so that larval foodplants or adult nectar sources for species known to be sensitive to fire are distributed among two or more burn units. Skips should be left unburned. Patchiness has its place in prairie sites; no native habitat type should be completely eliminated when reclaiming a prairie. Areas which are not threatened by woody invasion should be burned at considerably longer intervals than the areas that are problems. Along with a longer fire interval, other potential management tools should be used, such as mowing, grazing, and brush-hogging.

Rare butterflies may be just the tip of the prairie diversity iceberg. As with the hidden part of the iceberg, we don't know what endemic bees, tiger beetles, or jumping spiders may still exist down in the grasses on these remnants. Management that emphasizes biodiversity in the Loess Hills and in other prairie remnants can help us preserve more pieces of this rapidly vanishing ecosystem.

ACKNOWLEDGEMENTS

The author wishes to thank D. Cuthrell, J.C. Downey, J. Fleckenstein, J.C. Nekola, D.W. Schlicht, and G. Selby for their generous sharing of records. Access to sites was provided by The Nature Conservancy and the Iowa Department of Natural Resources, which also partially funded this research. Dennis Schlicht also provided access to state records, verified species identification, and inspired this research; without his help this paper would not have been possible. Also essential to this process were S. Spomer, C. Jacobs, and the anonymous reviewer who made many valuable suggestions.

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B.A.G.

SEQUENTIAL USE OF NICHE BY PRAIRIE OBLIGATE SKIPPER BUTTERFLIES (LEPIDOPTERA: HESPERIDAE) WITH IMPLICATIONS FOR MANAGEMENT

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Abstract. Data from prairie skipper (Lepidoptera: Hesperidae) flight times in the Loess Hills prairies suggest that resources are partitioned through time. In the same manner that an individual species utilizes various parts of a niche through its life stages, the combined prairie obligate skipper species utilize all parts of the niche at the same time. Eight species were observed to use 10 adults flight periods from April 19 to October 2, indicating that skippers may be present as egg, larvae, pupae, or adult at any date during this period. With all stages present, there are no management windows when skipper species are protected from possible detrimental effects of the chosen management regime. Comparison of the sequences in several prairies can indicate site richness and the effects of site history.

INTRODUCTION

Diversity has become an important factor in the evaluation of prairie areas. That diversity includes not only the hundreds of plants and many fewer vertebrates, but the most numerous group, the invertebrates. The true diversity treasure of any temperate environment is the arthropods and in particular the insects. Most interactions between prairie plants and animals involve insects, and, in most cases, these are obligate relationships. Those of us interested in the Lepidoptera are acutely aware that prairie skippers (Hesperidae) exist within narrow niche parameters and are even more endangered than the prairies on which they live.

The niche filled by adult skippers is for fast flying insects that use nectar as a food source. The larvae however have two separate niches. The Hesperiid type skippers have larvae that eat grasses and adults that are tanish, while the Pyrginae (Erynnis) skippers' larvae eat legumes and adults are dark-colored in two broods.

Misconceptions about the bionomics of Lepidoptera are evident, even among managers expressing concern for prairie invertebrates. In 1989 in a memo, an Iowa prairie manager stated that managers are concerned about the extensive use of fire when whole prairies are burned during the "active phase" of prairie insect life cycles. Insects are alive (active) all year not just during the time of adlut flight. The spring 1990 newsletter of the Wisconsin Bureau of Endangered Resources, The Niche (which is to be congratulated for considering the invertebrates), states that on one prairie, where the state-endangered Poweshiek Skipper, *Oarisma poweshiek*, is found, managers "leave about one of the five acres of skipper habitat unburned." For the rare Regal Fritillary, *Speyeria idalia*, "at least one unit with violets is left unburned." The stated purpose is to "...allow those rare species to seek shelter in the unburned areas or build up a population large enough to recolonize the burned area" (Martin and Hoffman 1990). It cannot be assumed safe to burn when adult invertebrates are not evident; eggs, larvae, or pupae cannot move to undisturbed patches.

These statements made us realize that we have data to demonstrate a phenomenon in prairie skippers that may help find methods of prairie management that will preserve diversity. This phenomenon is described here as *sequential use of niche*, a temporal sequence of adult emergence followed by eggs, larvae and pupae of skippers throughout the growing season.

METHODS

Study Area

The prairies from which this data was gathered were the relatively homogeneous northern Loess Hills prairies in the Sioux City area of western Iowa. They include Sioux City Prairie, Mount Talbot Prairie, and Five-Ridge Prairie, all in Woodbury or Plymouth counties. These multiple but not continuous hilltop prairies are surrounded by forest, agricultural land, or urban developments. They contain plants characteristic of the Great Plains, such as eared milkweed, *Asclepias auriculata*; lotus-flowered milk vetch, *A. lotiflorus*, dotted blazingstar, *L. punctata*; skeleton weed, *L. juncea*; and yucca, *Yucca glauca* (Nekola unpublished), as well as the more common big bluestem, *Andropogen gerardii*; little bluestem, *Schizachyrium scoparium*; and purple coneflower, *Echinacea augustifolium*.

Data Collection

The data was collected during the seasons 1986-1989 by the collection and identification of specimens of each species encountered. The data represented in the figure is a compilation of observations from all three prairies. Voucher material is preserved with the authors.

Species Studied

The skippers collected were prairie obligates, with the exception of the more cosmopolitan tawny-edged skipper, *Polites themistocles*. The eight species studied are presented in the order of first brood emergence (two are doubled brooded).

The mottled duskywing, *Erynnis martialis*, is a dark spread-winged skipper whose larval foodplant is New Jersey tea, *Ceanothus americanus*. *E. martialis* has two flights and overwinters as a mature larva that, therefore, would be a pupa or emerging adult during the spring burning season.

The wild-indigo duskywing, *Erynnis baptisiae*, also has two flights, the first during the spring burn season when eggs are laid on the *Baptisia* foodplants. The eggs will mature for the second flight in July. Full grown larvae overwinter (Opler and Krizek 1984).

Next to emerge is the dusted skipper, *Atrytonopsis hianna*. Its larval food plants are big and little bluestem. It overwinters as mature larvae from eggs laid in May and early June. It is the last of the dark (for thermo-regulation), spring skippers.

The tawny-edge skipper, *Polites themistocles*, uses prairies as well as most other grassy situations and might be one of two on this list to survive beyond the prairie ecosystem. The larvae eat grasses in the genus *Panicum* (Opler and Krizek 1984), and the immobile pupae hibernate (Scott 1986).

A denizen of quality prairie is the ottoe skipper, *Hesperia ottoe*. This large, as skippers go, ochre species uses both bluestems as larval foodplants. The larvae move from leaf-blade shelters to buried hibernation shelters in the fourth instar (Dana 1989). They are probably safe from early fires.

The beard-grass skipper, *Atrytone arogos*, is the smallest of the sequence. The larvae feed on big bluestem from tents of two leaves sewn together and hibernate as fourth instar larvae and would be in that stage during early spring burns. They pupate one meter above the ground (Opler and Krizek 1984), and the eggs are laid on grass blade tips in July.

One of the most widespread prairie skippers in the crossline skipper, *Polites origenes*, which flies from late June to mid-July. The larval foodplant is said to be little bluestem and other grasses. It overwinters as a third instar larvae (Scott 1986).

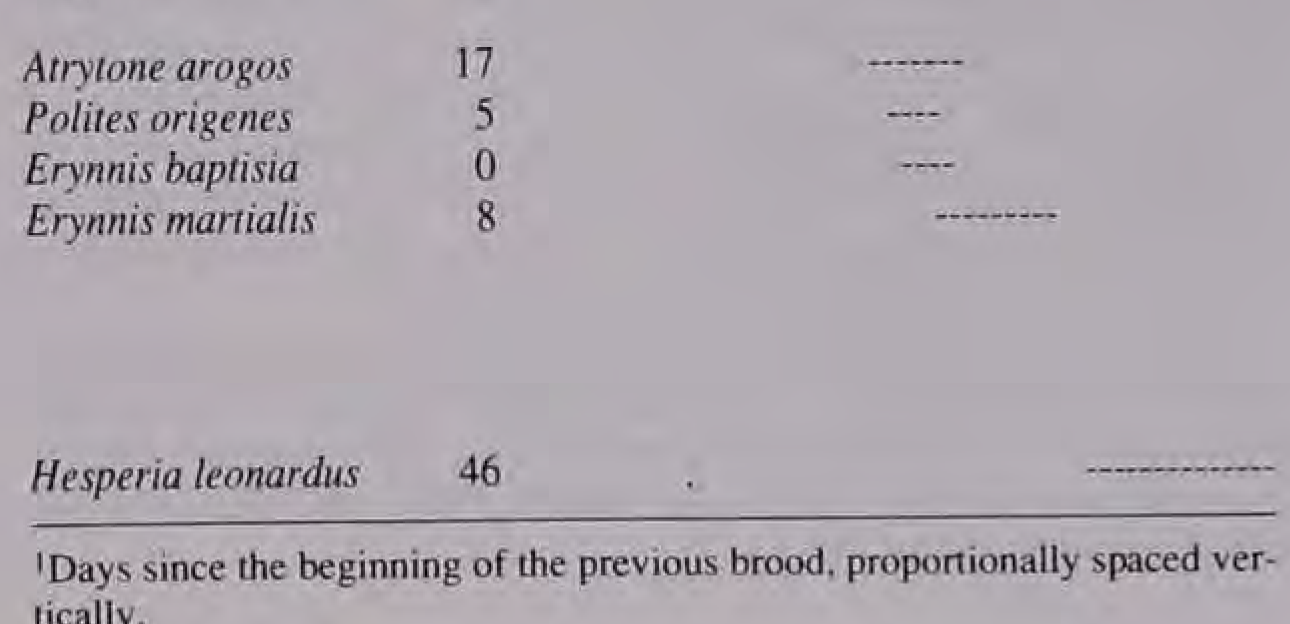
Leonard's skipper, *Heperia leonardus*, stands the last watch of the season and for that reason hibernates in the least developed form, the first instar after hatching, and would be vulnerable in the spring. The larvae are said to eat Sswitchgrass, *Panicum virgatum*; the adults are associated with blazing star.

RESULTS AND DISCUSSION

Using data gatherd by Orwig in the three Loess Hills prairies, we plotted the sequence of emergence, and flight duration for these prairie obligates. When emergence date was plotted against the time between species emergence, the result was a line of predictability (Figure 1). The emergence date of the next (or missing) species as well as the stage of life cycle at any particular date can be inferred by correlating the date to the life cycle position on the chart. The adult is preceeded by the pupae and is followed by the egg and larval stages.

The skippers are sequentially using part of the same niche, as evidenced by their stagered emergence, even though the adults flights overlap. There are several possible reasons for this. The first is competition for adult flight space, which includes the use of dominant composites as landing sites to defend territory for mating, most of which happens in the first few days after emergence. The second is competition for sites of oviposition on the requisite foodplants, which also happens shortly after emergence. The third is the use of food plants by the various species of larvae, each at a different stage (on the site), even though larval foodplant is not a limiting factor. The fourth is the availablity of safe hibernation sites for all of these species. The last is that there is extensive competition for nectar. Evans (1986) reports that an average of 36.2 bee species used each of 19 species of flowers on Evans Old Field, Livingstone County, Michigan. As a result, these insects may be sequencially using the niche to utilize the supply of nectar from various plants throughout the growing season. This has the benefit of providing pollinators throughout the season to help serve the continuous bloom on the prairie.

Figure 1. Sequential use of niche by prairie obligate skippers in Iowa Loess Hills, 1986-1989.



[1] Days since the beginning of the previous brood, proportionally spaced vertically.

The concept of temporal dissociation (in our case of adult emergence and subsequent life stage staggering) was described by Clench (1967), but because of heterogeneous habitat, he divided the skippers into three sets to find dissociation. Shuey (1986) refuted his findings based on the habitats Clench chose to demonstrate. We believe the Loess Hills prairies fill Shuey's expectations. First, they are a rare habitat, isolated by abiotic factors that allow little genetic influx from other habitat types, and second, the competition array is homogeneous so that similar ecological requirements allow a sequence of similiar species.

CONCLUSIONS

Management Implications

In the same manner that an individual species utilizes various parts of a niche through its life stages, the combined prairie obligate skipper species use all parts of the niche at the same time. Select any date in Figure 1 and follow it vertically and you will find one or another insect in all possible stages of metamophosis (egg, larvae, pupae or adult). There are no open times when invertebrates will not be affected. In fact, the times when the adults of the species in question are flying are as free of risk as any other time.

The solution is to spread the risk by using multiple management techniques at different times. Furthermore, the method must be applied in patches that are smaller than the patch of plants that the obligate invertebrate uses. If a large prairie is divided and treated in only a few units, the effect will be to reduce the invertebrate diversity to a level that is much like a small prairie with only a few habitat patches. Dana (1989) found that some skippers have a natural mortality of 50% to 60% without management considerations. If only 1/5 of its habitat is safe, accidental loss will surely occur. As some species might fly only 50 or so individuals on a prairie, a small area may contain most of the population.

Leopold said that the first rule of intelligent tinkering is to save all the parts—in this case the species. John White states further: before tinkering, set aside a working model—the ecosystem (White 1986). Let us proceed cautiously and with knowledge of all components of the prairie.

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THE FIRE HISTORY OF SCOTTS BLUFF NATIONAL MONUMENT

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Abstract. Determination of presettlement fire return interval, seasonal occurrence of fire, and estimation of fire intensity is difficult in grassland ecosystems, which lack woody plants to carry fire scars. A review of published scientific literature, historical journals, diaries, narratives, letters, military records, eye witness accounts, and National Park Service fire records was conducted to reconstruct a fire history for Scotts Bluff National Monument (SBNM). Fire history prior to 1935 was determined for the general land area west of the confluence of the North Platte and South Platte rivers to Fort Laramie Wyoming, north to the Black Hills and south to the Kansas border. For the period after 1935, the review concentrated specifically on SBNM. The presettlement fire return interval was estimated at 15-30 years, and fires occurred primarily in the dry season—late summer and early fall. In contrast, the postsettlement fire return interval was greater than 50 years, and fires occurred in the spring. Fire intensities were greater in presettlement fires. Prescription burning for management of natural areas should probably mimic presettlement fire characteristics in order to have the same ecological influences on community composition.

INTRODUCTION

Grasslands of the Great Plains developed and were maintained by seasonal periods of aridity that created flammable fine fuels in sufficient quantities to propel natural and man-made fires through grassland ecosystems (Albertson and Weaver 1945, Stewart 1953, Kucera 1981, Axelrod 1985). Fire is, therefore, an important force in the regulation and maintenance of species composition in grassland ecosystems (Daubenmire 1968, Vogel 1974).

The vegetation of Scotts Bluff National Monument (SBNM) has probably undergone change in species composition over the past 200 years because of alterations in the fire return interval, in seasonal occurrence of fires, and in fire intensity. These factors have been found to influence the floristic composition of the northern mixed prairie (Shantz 1947, Dix 1960, Wright and Bailey 1982, Bock and Bock 1984, Smith et al. 1985, Mihlbachler 1986, Steinauer and Bragg 1987). Invasions of grasslands by fire-sensitive woody plant species have been associated with lengthened wildfire return intervals (Kucera 1981). Harrison (1980) and Steinauer and Bragg (1987) observed the invasion of ponderosa pine (*Pinus ponderosa* L.) in Sandhills prairie south of the Niobrara River in north-central Nebraska. Fisher et al. (1986) concluded that woody plants have invaded sites historically occupied by grassland or savanna ecosystems at Devil's Tower National Monument in northeastern Wyoming. More subtle changes in herbaceous species composition on grasslands also occur as a result of alterations in fire return interval, season of fire occurrence, and fire intensity (Dix 1960, Conrad and Poulton 1966, Daubenmire 1968, Wright and Bailey 1982).

Because of a lack of trees to carry fire scars, there are few reliable published summaries of natural fire attributes in the northern mixed prairie (Wright and Bailey 1982). Further, the fire accounts which do exist are often incomplete and contain limited information regarding exact time, location, size of fires, and estimated fire intensity. However, defendable estimations of presettlement fire return intervals, seasonality, and fire intensity can be inferred from the combined use of historical references and recently published fire history literature.

The objectives of this research were to determine fire return intervals, seasonal occurrence of fires, and relative intensity of fires prior to and following settlement of SBNM.

METHODS

The fire history of SBNM was reconstructed by reviewing published literature, historical records, and National Park Service (NPS) TF-1202 fire records for SBNM. For the period prior to 1935, the review of historical records and published literature was conducted for the land area situated west of the confluence of the North and South Platte rivers to Fort Laramie Wyoming, north to the Black Hills and south to the Kansas border. Literature from this period was reviewed on a regional basis because few fire records specifically referred to SBNM. For the period following 1935, the fire history review concentrated specifically on SBNM because of the existence of NPS fire records.

Records from the Henderson collection of Oregon Trail Records (University of Wyoming Archives Collection), the Wyoming State Historical Society (Cheyenne, Wyoming), and the Cook collection (SBNM Nebraska) were searched. For the period prior to 1935, 759 historical records were reviewed including journals, diaries, narratives, letters, military records, and eyewitness accounts. The source, location, date, size, cause, and observer of each fire was recorded and stored in a Data Base Three Plus format. A copy of the data base is located at the SBNM library. In addition, we reviewed recently published literature pertaining to presettlement fire return intervals for the region.

Postsettlement fire return intervals for SBNM were determined by comparing the boundaries and dates of all fires that occurred on the Monument on a system of overlay maps. Intervals were calculated as the lengths of time between fires occurring at the same points in space. The park, thus, consists of a mosaic of different fire return intervals.

RESULTS

The majority of western pine forests have fire return intervals ranging from sixty to several hundred years (Weaver 1951, Wagener 1961, Houston 1973, Hall 1976, Arno 1978, Romme and Knight 1982). In contrast, fires were far more common in grasslands. Wright and Bailey (1982) concluded that a natural fire return interval as low as five years was probable for grassland ecosystems having level to rolling topography. However, where more topographic variety exists, like SBNM, the fire return interval was suggested to range between 20 and 30 years (Wright and Bailey 1982).

Fire return intervals have been evaluated for several sites near SBNM. Steinauer and Bragg (1987) reported that fire return intervals in the Nebraska Sandhills (100 km northeast of SBNM) had lengthened from 3.5 years between 1851 and 1900 to 8.5 years between 1901 and 1950. Using dendrochronolgy techniques, Shilts et al. (1980) estimated fire return intervals in grasslands of Wind Cave National Park (90 km north of SBNM) for the time period between 1820 and 1910 to be 13 to 21 years. Perhaps the most detailed work done to date estimating presettlement fire history in the northern mixed prairie is that by Fisher et al. (1986). Based on fire scar research at Devil's Tower National Monument (185 km northwest of SBNM), they concluded that between 1600 and 1770 the fire return interval was 27 years, from 1770 to 1900, the fire return interval was 14 years, and after 1900 the fire return interval lengthened to 42 years. We conclude that fire return intervals in the northern mixed prairie prior to 1935 were about five years on smooth and gently rolling topography and 15 to 30 years on topographically diverse areas like SBNM.

NPS fire records from 1935 to the present indicate that the average fire return interval is greater than 50 years on SBNM (Table 1). In fact, more than 45% of the Monument has not burned since 1935, and less than 10% of the park has a fire return interval of 27 years or less.

Table 1. Fire return intervals for Scotts Bluff National Monument from presettlement to present time.

Time period	*Average interval (years)*	*% Park area burned*
Pre-1935	15.0-30.0	100
1935-1969	14.0	<1
	34.0	19
	Unburned	81
1970-1990	6.6	1
	10.0	4
	20.0	41
	Unburned	54

Since settlement, the fire season has shifted from late summer to early spring (Figure 1). Over 70% of the fires sighted in the SBNM region between 1824 and 1934 were recorded between July and November with most occurring in July and August. Between 1935 and 1969, a slight decline in late summer fires was observed, and from 1970 to 1990, a dramatic shift from late summer to spring fires (March-June) occurred.

Pioneer travel in western Nebraska was mainly in the spring because wagon trains passed through the region early in the year in an attempt to reach and pass through the western mountains before the onset of winter conditions. Of the 759 pre-1935 historical records examined in our investigation, only 85 records were from summer (July-September) travelers in the SBNM region, whereas 610 records were from spring travelers. Even with such a strong bias toward travel and increased observation opportunities during spring, spring fires were rarely observed.

Spring and early summer fires are generally less intense than late-summer and fall fires (Wright and Bailey 1982). This is due to higher soil water content, higher fuel moisture, lower soil temperatures, lower ambient air temperatures, and higher relative humidity. Overall, the shift to spring-season fires resulted in less intense fires.

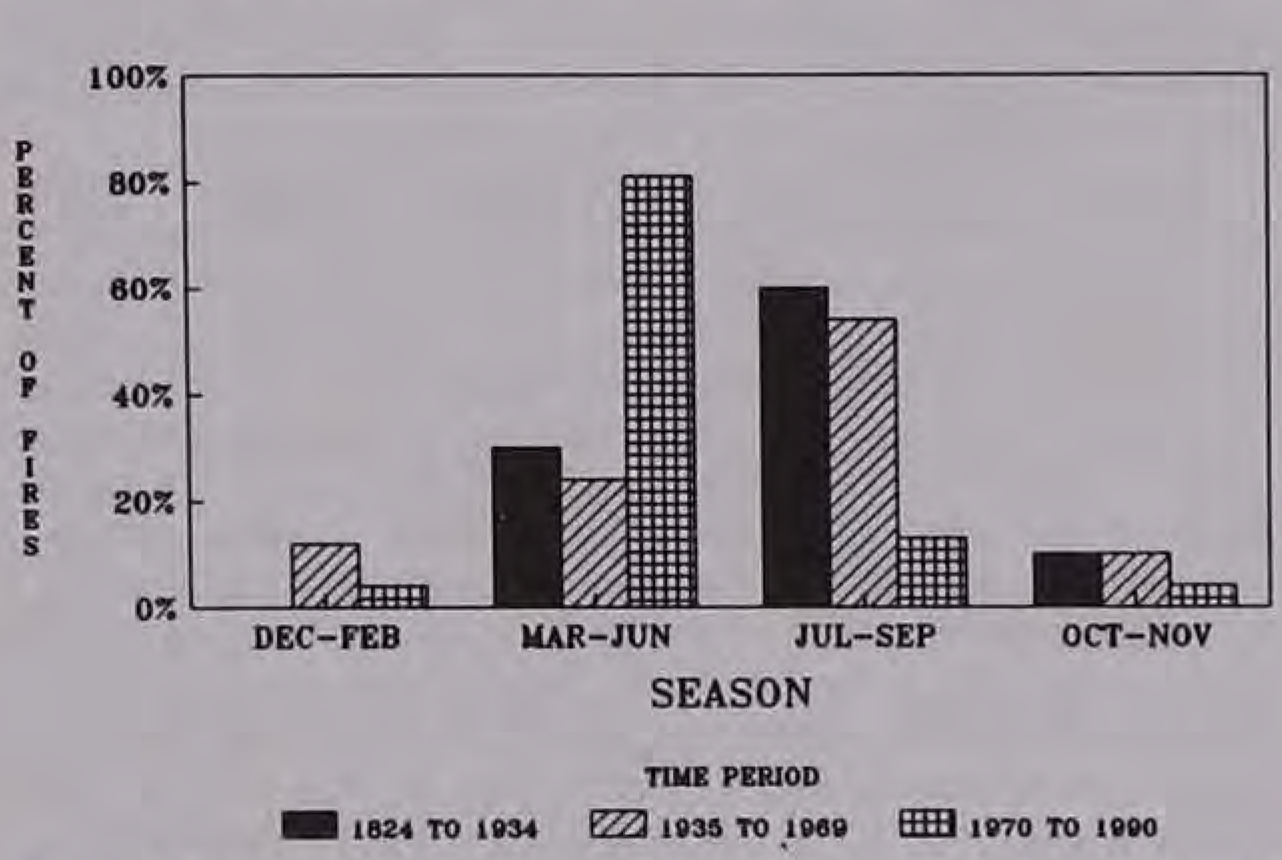

Figure 1. Change in seasonal occurence of fires for Scotts Bluff National Monument, 1824-1990. Based on observations of 10 fires in 1824-1934, 26 in 1935-1969, and 46 in 1970-1990.

DISCUSSION

Following settlement, the fire return interval for SBNM lengthened to 54 years or longer for more than 90% of the SBNM land area. This is attributed to European settlement and the advent of accidental and intentional fire suppression. The increase is similar to changes reported for other grassland areas following settlement (Shilts et al. 1980, Wright and Bailey 1982, Fisher et al. 1986, Steinauer and Bragg 1987).

The shift from late summer to spring fires was somewhat unexpected. Between 1935 and 1969 managers attempted to suppress all fires within Monument boundaries. The dramatic shift from dry to wet season fire between 1970 and 1990 resulted from the introduction of prescription burning and the suppression of all wildfires. Current NPS prescribed fire management policy for SBNM permits managers to conduct prescribed burns in the spring. The rationale is that spring burns are easy to control, revegetate quickly, and leave a mosaic of burned and unburned areas.

The NPS is mandated by Congress to manage the vegetation of SBNM to resemble presettlement species composition and diversity. Because fire is a significant force in structuring plant communities, management techniques that lengthen the interval between fires, shift fires from summer to early spring, and/or reduce fire intensity by prescribing cooler fires may result in species composition shifts toward fire intolerant and potentially undesirable non-native vegetation.

Prescribed burning programs for this and other grassland areas where fire is used to restore or maintain historical balance among species must consider the ecological impact of changing fire return intervals, season of burning, and fire intensity. The reintroduction of fire at the natural fire return interval but during the wrong season of year or at the wrong intensity may not result in restoration or maintenance of the native plant community. Unless evidence to the contrary is found, we recommend a prescription that mimics the presettlement fire history—high intensity summer fires on a return interval of 5 to 30 years.

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USE OF PORTABLE ENGINE PUMPS IN PRESCRIBED BURNING

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Abstract. During prescribed burning, the Wisconsin Department of Natural Resources-Bureau of Endangered Resources-Natural Areas Section uses portable engine pumps whenever possible to provide additional safety, to reduce fatigue on individuals, and to decrease burning time. The use of these pumps has allowed us to burn some areas that, in the past, were difficult to burn. A pump can be carried by two people and can pump up to 662 liters of water per minute through 2.5 cm hose for 244 m. Water is pumped from an open water source or from a well point when water is close to the surface. When burning along small streams, pumps can be carried in canoes or boats, and water can be pumped directly from the stream.

INTRODUCTION

One objective of prescribed burning is to burn the desired area as safely and efficiently as possible. Any equipment that helps reach that objective without jeopardizing the site's natural integrity should be used.

Wisconsin Department of Natural Resources' fire control personnel use hand-carried engine pumps in fire control whenever feasible. Pumps are used on peat fires and on fires where water is nearby. The Department's Bureau of Endangered Resources-Natural Areas Section has adopted this idea and now uses portable engine pumps whenever possible in prescribed burning.

This paper provides basic information on using small engine pumps in prescribed burning.

METHODS & MATERIALS

Methods

Before using this system, we recommend extensive planning and consultation with someone experienced with portable fire control equipment and the use of small engines. It may be beneficial to conduct field tests before purchasing any equipment because pumps can vary widely in price and performance. More expensive, small pumps that can pump a high volume of water farther than 250 m are available.

Pumps can be carried by two persons, but a carrying support can be constructed for ease of handling. A solid support, such as a board, is necessary when the pump is placed on wet ground. The pump must be primed before starting, and tight connections must be maintained. Practice using the equipment before a fire and be sure everyone is trained to use all the equipment.

Small engine pumps are useful whenever water is close enough to be pumped. Lakes, rivers, creeks, sloughs, and potholes all provide usable water. If below ground water is close enough to the surface, as in many wet to wet-mesic prairies and sedge meadows, a well point can be sunk, and water can then be pumped from it. The wells can be driven into the ground with a maul/post driver or forced (jetted) in with water. We have pumped water from a well sunk to a depth of 2 meters. If plans are to construct well points, check regulations regarding their placement. In Wisconsin, permits are required before placing wells in a floodplain.

We are able to pump enough water to extinguish a fire through 244 m of hose. In many cases, water can be pumped in two directions, providing up to 488 m of firebreak.

All hoses should be laid out before burning. Sections can be hooked up as needed by idling the pump. We maintain radio contact between the pump operator and the crew controlling the fire. It takes practice and coordination to control the hose when burning and moving equipment. It is necessary to keep the hose free of kinks, which reduce water flow. If the pump is being carried in a canoe or boat along a stream, use less than 15 m of hose for easier handling.

To help construct a firebreak, we wet down a 30 m linear strip before fire is brought along the line and then keep ahead of the firing line by an equal amount to provide a safety factor. Additional equipment is necessary: a back-up pump and nozzle, as well as mobile back-up equipment, such as backpack water pumps.

After the burn, the equipment must be properly dried and stored. Hoses take time to wind up, and a small wooden device can be made to help wind the hose. Hoses must be thoroughly dried.

Basic Pump Materials

1. *Small Engine Pump with a 2-or 4-cycle engine.* We use 205-cc, 4-cycle pumps that can pump 662 liters of water per minute. A 4-cycle pump costs about $500.
2. *Hose.* The 30 m hose we use is 3.8 cm in diameter and is double-lined. Each 30 m hose costs about $70.
3. *Box Strainer and Hose Attachment.* A heavy duty box strainer is placed in the water and a 3 m suction hose provides attachment to the pump. Strainer and attachment cost about $35.
4. *Nozzle.* We use adjustable nozzles that can deliver a stream of water or a spray. Nozzles cost about $25.

Well Materials

1. *Well Point.* Well points are 60 gauge, flush sand points. These points can be pulled out more easily than other types of points. Easy removal facilitates reuse of points in areas where temporary wells are preferred over permanent installations. Points cost about $50.
2. *Galvanized Pipe.* All pipe used is 3.175 cm and threaded. The pipe is attached to the well point with a coupling and capped 1.5 m above ground. Galvanized pipe runs about $4.00 per meter. Cutting and threading are additional costs.
3. *Pitcher Pump.* A hand pump is used to prime the well before pumping. This sink hand pump can be obtained through hardware stores and costs about $50.

DISCUSSION

The use of pumps has allowed us an opportunity to burn in areas that were previously difficult to burn, such as wetlands with heavy fuel loads. Areas that burned frequently before settlement can now have a simulated burn regime reinstated. The pumps have allowed us to break some large burn areas into smaller units. These smaller units are necessary in many cases to protect fire sensitive species whose continued existence may be jeopardized by burning the entire area.

Using these small engine pumps has made prescribed burns safer because a large volume of water can be pumped. Fire control is easier, and any escaped fires can be extinguished more quickly. This tool has also reduced fatigue in personnel, who in the past had to carry backpack water pumps. In addition, on sites previously burned by labor intensive methods, the pumping system permits a much safer and more cost-effective burn.

USE OF NATIVE VEGETATION IN ROADSIDE LANDSCAPING: A HISTORICAL REVIEW

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Abstract. Today many midwestern states are experimenting with the use of prairie plantings along their highways. The rationale behind these programs varies but often includes maintenance concerns, erosion control, aesthetics, and recovery of regional identity. In this paper, we explore the ideas of individuals who, in the first three decades of this century, proposed planting our highway rights-of-way with native plants. We look at their goals, compare them to our own, and see how they apply to the future of naturally landscaped roadside programs.

INTRODUCTION

The conference theme, "Recapturing a Vanishing Heritage," expresses the sense of urgency and delight that lies at the heart of our current attempts to preserve, restore, and manage our midwestern prairie landscape. In a similar sense, it also highlights the increased interest that state transportation departments have in planting ecologically appropriate groupings of native species on state and county highway rights-of-way. The promotion of native species for rights-of-way landscaping, however, is not a new phenomenon but rather a return to ideas and policies first promoted when automobile travel began to flourish in the 1920s and 1930s.

In this paper, we explore ideas espoused by landscape architects and plant ecologists, regarding the natural landscaping of roadways, and how those themes have changed over time. We suggest that historic arguments based on aesthetics, function, and ecology each have merit and can provide us with a reliable platform upon which to build, rather than simply re-learn, constructive ways to incorporate indigenous vegetation into our lives.

METHODS

We reviewed more than 50 papers about highway landscaping published in popular magazines, professional journals and proceedings, newsletters, short-course materials, and books during the period from 1910 through 1989. We then drew themes from the central ideas of the authors and related them to current thinking about rights-of-way planting.

DISCUSSION

Early Landscape Themes and Proponents

Between 1900 and 1940, various individuals advocated and implemented a regional style in the midwestern prairie states—a style that emphasized native plants in homes, campuses, parks, and along newly constructed roadsides. These men and women sought, first, to protect existing native plants and, second, to use native plants and plant groupings in landscaping situations, such as roadside development.

In our examination of written documents, we found three themes emerged throughout the writings of these early supporters of naturally landscaped roadsides. First, these advocates saw roads and roadside development as part of a larger social issue—the necessity for a stable, aesthetically pleasing, and economically healthy rural America. Second, many envisioned the engineered road and its impeccable roadside as a symbolic loss of the region's identity and its pioneer spirit. Last, some recognized that the then emerging science of plant ecology could, when combined with artistic purpose, lead to some very exciting opportunities to recapture the aesthetic appeal and symbolic strength of the prairie landscape.

Roadside development in the rural landscape.

The first theme has natural ties to the Jeffersonian ideals of agriculture and to the farmer as a mainstay in the American economy and way of life. By the end of the 19th century, the Country Life Movement, an organization whose members feared this ideal was slipping away, had formed and began to gain influence in both national government and at many Land Grant colleges (Kirkendall 1986). One of the many improvements they worked for was the betterment of rural roads. With the passage of the Smith-Lever Act in 1914, which the Movement strongly supported, came the growth of the college Extension Service: the scientific and educational tool necessary to communicate the group's ideas to the rural community. Advocates of naturalistic roadside planting, such as Wilhelm Miller (University of Illinois at Urbana), Frank Waugh (Massachusetts State College), Franz Aust (University of Illinois at Urbana as Miller's assistant, and later University of Wisconsin-Madison), and P. H. Elwood, Jr. (Ohio State University and Iowa State College), worked within the Extension setting to enhance the rural landscape for those who lived and visited there.

In 1912, Wilhelm Miller, who was trained as an editor and horticulturalist, came to the University of Illinois with definite ideas about the prairie landscape and its importance in developing a rural midwestern "sense of place" among agricultural settings and along roadsides, a program he called "The Illinois Way". In a speech to the Illinois Highway Commission, he said:

> It is a mistake to suppose that our greatest financial asset is something rare, remote and spectacular, like Niagara, Yosemite and Yellowstone...To the ninety million inhabitants of the United States, the most important scenery is the common, everyday, familiar scenery in which we pass our lives...The most important scenery in the world is roadside scenery, because it affects the most people.
>
> Miller 1913

Arguing for functional as well as aesthetic transportation routes. Miller portrayed the needs of a county in Illinois as follows:

> [Its] roads are muddy enough to kill a horse, and there is nothing to see along the highway; every shrub and flower has been cut down. There is nothing to soften or relieve the cast iron system that laid out the country in absolute, unvary-

> ing squares....How can this be improved...and at the least expense?
>
> Miller 1913

Miller demonstrated through his extension work how fundamental planning and planting could improve the rural landscape and thus, rural life. He and Franz Aust developed the "Illinois Way" into a variety of planting motifs and implemented them in rural models, such as the prairie motif they employed at the farm of Harvey J. Sconce in northeastern Illinois. Miller wrote of the situation:

> The main problem of the Sconce planting is to idealize the prairie views, for although these are very fine from the standpoint of farm management, they are perfectly flat, and like other extremely valuable agricultural land, are generally devoid of trees and shrubs. To restore as much as possible the old prairie magic, Mr. Sconce is framing broad views of corn and wheat with 'symbols of the prairie,' i.e. plants with strongly marked horizontal branches such as Scarlet Haws, Prairie Crab Apples, Honey Locust, and Sassafras.
>
> Miller 1915

Miller also publicized the ideas and work of landscape artists Ossian Simonds and Jens Jensen, both of whom had much earlier used native plants in their designs. Simonds emphasized the need to create a harmony between the roadside and adjacent properties, especially by providing openings that displayed distant views (Simonds 1915). Jensen, meanwhile, stressed that

> Roadsides are all important in the development of the rural country. It is from our highways that we get acquainted with our country—from our highways we see its beauty and are inspired by it.
>
> Jensen 1924a

P. H. Elwood, Jr. oversaw one of the first college courses devoted to training young people in roadside development and planting. While he believed in the power of beauty, Elwood viewed the roadside landscape first as functional, then artistic:

> Successful landscape extension must first of all satisfy practical and economic requirements before it becomes a work of art. We have already had too much hitching 'the cart before the horse,' trying superficially to beautify something organically and fundamentally bad.
>
> Elwood, Jr. 1922

Loss of regional identity and pioneer spirit.

The need to balance the engineered road and its manicured roadside with the pioneer spirit and thereby avoid the symbolic loss of the region's identity also concerned many of the writers. Among those we read, Jensen set the overriding tone when he wrote

> It is a fine art to paint beautifully, but it is a greater art to produce a living picture where the cultivated and the primitive have been merged into a great ensemble
>
> Jensen 1924a

Miller's "Illinois Way" was based on an idea of maintaining strong, symbolic ties with the past, as he emphasized when he wrote:

> The guiding principle is to restore and intensify the native beauty of each locality....Every soil type tends to have its characteristic trees, shrubs, and flowers
>
> Miller 1913

But he was disturbed about the obsession to control our natural surroundings:

> Our present law encourages the destruction of every native bit of roadside beauty because it puts the work of destroying weeds into the hands of men who make no distinction between pests and harmless wild flowers. These men have only one conception of beauty—a neat, close-cropped strip of grass....Therefore, the control of roadside weeds and roadside planting should be put in the hands of public spirited men of knowledge and taste....
>
> Miller 1913

Jensen also saw the region as forming the basis for roadside development:

> All roadside planting should be determined and based on the country and its native vegetation through which the road winds its way. In this way the roadside planting will become a part of the general landscape and enhance the beauty of its surroundings as far as this is possible for a highway to do
>
> Jensen 1924b

In particular, and to an extent that exceeded Miller's, Jensen made it clear that such plantings must be exclusively native:

> To make the roadside planting a part of the native landscape means to plant native plants—such plants as grow in the region of which the road is a part....Where the highway runs through open country framed by imposing landscapes, groves or groups of trees are the only solution. These groves should consist of one tree type with low-growing shrubs or flowers at intervals....On sandy lands we may have an entirely different picture with such plants as pines, cedars, creeping juniper, bittersweets, grapes, numerous grasses, butterfly weeds, lupines and prairie clover.
>
> Jensen 1924a

Despite this advocacy for a midwestern motif and the aesthetic elements of the prairie—its openness, horizontal lines, the grasses and wildflowers as they changed over the seasons—little actual planting with prairie species took place along newly developed roads. It appears that a growing urban population and its appreciation for a highly engineered, streamlined aesthetic merged with technical advances in turf propagation and management to supplant the prairie motif.

Jensen, nevertheless, remained hopeful when he wrote in 1932:

> They have long vanished from along our highways, but perhaps someday the Department of Highways will restore our prairie flowers along our roads and it is hoped they will restore many of our other interesting prairie plants that once grew there.
>
> Jensen 1932

Frank Brandt, a student of Aust's at Wisconsin, reviewed writings that promoted naturally landscaped rights-of-way prior to 1930. He also conducted a survey of 14 state highway commissions to determine their philosophies and roadside landscaping practices (Brandt 1931). His findings testify that a truly rural, prairie right-of-way landscape had become a static idea that was quickly losing ground to mechanized progress. In a series of recommendations Brandt proposed

1. Each state should develop a number of planting motifs based on the individuality and character of the particular physical environment through which the highway might pass.

2. Highway rights-of-way should be wider with shallower, broader, meandering ditches. This width would encourage cluster rather than single row tree planting.

3. Roadside planting should be carefully planned so as to bring the surrounding landscape into the roadside design instead of trying to form a separate design within the rights-of-way limits.

4. Plants for rights-of-way plantings should be judged with regard to their fitness and hardiness, potential for artistic design, and maintenance costs. Foreign plants should be discouraged since they would not harmonize with surroundings nor always adapt or be easy to maintain.

5. Existing native plant growth including community remnants should be preserved.

Thus, in the 18 years between Miller's (1913) and Brandt's (1931) writings, no one had addressed the means or developed the policies to go beyond simply hoping to use indigenous plants as part of roadside plantings.

Plant ecology and roadside design.

The third theme is the potential for plant ecology to contribute scientific support for landscaping roadsides with native plant groupings. Plant ecology came into its own during the first two decades of this century, producing researchers and scholars such as Frederick Clements and Henry Cowles in the Midwest (McIntosh 1985, Tobey 1981). These men and their colleagues developed theories (such as physiographic ecology, succession, association, and climax) and sampling methodologies (quadrat sampling, frequency indices) to explain and investigate the relationship of plants to their environment. Others then began the slow process of incorporating the principles of plant ecology into roadside planning and design. Two of these individuals were Wilbur Simonson and Frank Waugh.

Simonson, a senior landscape architect with the United States Bureau of Public Roads, wrote numerous articles during the 1930s on right-of-way landscaping. Whereas previous landscape architects talked about roadside plantings in terms of preservation and aesthetics, Simonson emphasized the need for naturalistic plantings as a matter of economics, based on an understanding of conservation and an area's ecology (Simonson 1934, 1936). According to Simonson, a systematic pre-construction survey of the native flora on rights-of-way and the lands adjacent to highways would indicate the most appropriate plant materials to use (Simonson 1936). This would assure that the highway would not only fit into the landscape but that the landscaping would be cost-effective.

Waugh not only taught, he spent considerable time during the 1920s and 1930s doing pioneer work siting and landscaping U.S. National Forest roads, including the Mount Hood scenic drive in Oregon (Taylor 1943). As early as 1917, he began to include plant ecology in his aesthetic writings (Waugh 1917). While others, like Miller and Jensen, discussed the need to place plants where best adapted, Waugh used the scientific concepts of plant community ecology to become much more specific. In 1931, he wrote an article entitled "Ecology of the Roadside" in which he described the ecological influence of the roadway on the surrounding flora. The article emphasized the zonal distribution of flora as influenced by "edaphic conditions, moisture, and light relations...." Using this idea of plant group zones, Waugh suggested that the highway landscaper "should be able to achieve a result at least scientifically more accurate than the planting plan developed...in the drafting room" (Waugh, 1931). Waugh was the first to propose that ecological studies were necessary to restore or create natural plant communities along roadsides.

Waugh was also influenced by a book written by a plant ecologist and a landscape architect, *American Plants for American Gardens*. Its introduction states

> The study of native plants in relation to their environment brings out the fundamental principles upon which the indigenous vegetation is established, and the contribution that an understanding of these facts can make in the retention or recreation of the natural landscape.
>
> Roberts and Rehmann 1929

One of its authors, Elsa Rehmann, later argued that roadside engineers and managers needed an education in plant community ecology to properly perform their tasks. She further suggested that these professions needed to develop a respect for native vegetation, and she was critical that they tended to be "overactive in clearing along roadsides."

Rehmann 1933

Aust, as Chairperson of the Wisconsin Chapter of the Friends of Our Native Landscape, led that group to cooperate "with the Highway Commission in the protection of the existing scenic beauty along our highways." Aware of the problem posed by Rehmann, he opted for an ecological solution:

> Educational talks should be given on the things along the highway which should be saved and also instructions given regarding the time of the year that certain rights-of-way may be cut without injuring the wild flowers.
>
> Aust 1932

While these ideas were sound, they were only pioneering attempts. Certainly, the limited availability of propagules for many native plants and a lack of understanding of how to establish and manage such plantings may explain the lack of enthusiasm in many state transportation departments. However, professional designers and engineers also lacked the ecological understanding necessary to make the prairie roadside a reality. For example, a roadside planting plan by Charles Le Sure, an Illinois landscape architect inspired by Miller and Aust's work, demonstrated little knowledge about how to establish and maintain native prairie species (Le Sure 1923). Many of the prairie wildflowers and grasses that Le Sure depicted in a plan for a natural roadside would not have been able to thrive due to the shade cast by the plan's dense tree canopy.

It was not until the late 1930s that prairie ecologists, like Ted Sperry, along with Civilian Conservation Corps workers, began the first known prairie restoration, now the Curtis Prairie at the University of Wisconsin-Madison Arboretum. Work and research on this prairie slowly and quietly began to answer some of the questions concerning prairie establishment and maintenance, especially the importance of fire as a management tool. Shortly thereafter, at the same arboretum, University of Wisconsin botanist Henry Greene single-handedly created the prairie that bears his name. It, too, provided a welcome source of information regarding the possibility of restoring the beauty of the prairie environment. Other restorations in Illinois, at Knox College, at the Morton Arboretum, and at Fermilab, followed during the 1950s and 1960s. Information from these restorations was used by others to conduct restorations for numerous conservation parks, nature centers, schools, and residences. This activity swelled interest in the prairies and other native communities tremendously, encouraging the development of private native plant nurseries and providing a better understanding of how to recreate the prairie community. With this knowledge and support, planners could now realistically begin to assess the use of prairie species as useful vegetation for highway plantings.

Present and Future Right-of-Way Planting and Policy

Today, the public assumes that roads will be safe, allow rapid traffic movement, and be relatively economical in their construction and maintenance. Within those constraints, a variety of reasons have been given to justify the use of native plants instead of traditional plantings along roadsides. These include greater erosion control, lower maintenance costs, greater adaptability to climatic extremes, enhanced aesthetics, and the ability to reclaim, if only symbolically, a state's regional context or heritage. Thus, it appears that earlier themes of social health, regional heritage, and aesthetics, while still viable, have been diminished by more functional purposes. Nevertheless, even traditional management techniques that focus on controlling instead of encouraging vegetation may no longer be applicable. James Ritzer recently suggested that our perspective of roadside management needs to change:

> A roadside program dedicated to preservation of the roadside resource should place as much or more importance on plant performance as on plant control. A program emphasizing controls presumes that there is something to control.
>
> Ritzer 1990

To place emphasis on preservation and management of existing vegetation, however, managers must begin to re-educate themselves as to consequences of their actions on that vegetation: an idea Elsa Rehmann suggested nearly 60 years ago.

Beginning in 1968, midwestern prairie ecologists, entomologists, landscape architects, and other prairie enthusiasts began to meet at biennial conferences to share their experiences in creating artificial grasslands and managing extant sites. The energy and ideas of this group helped spark what has since come to be known as restoration ecology. This new discipline is based on the premise that we can learn more about species and their ecosystems by asking questions and testing ideas about how to actively restore them to a previous condition (Aber and Jordan 1985).

One interesting use of the restoration ecology approach to roadside development is the program described by Gayle Weinstein in her report for the Denver Botanic Gardens (Weinstein 1988, 1989). Her paper, at the 1988 North American Prairie Conference about establishing a research program for the restoration of short to midgrass prairie along Colorado Highway 121, included several recommendations that begin to bring the role of restoration ecology into rights-of-way landscaping:

1. Establish plant selection criteria based on ease of establishment, availability, aesthetics, erosion control capability, adaptability, genetic purity, and natural community composition.
2. Evaluate previous research, methods, and techniques and their costs.
3. Specify the successional stages of the plant community desired and understand its dynamics and limitations.
4. Evaluate, monitor and maintain records of planting attempts, their success and cost.
5. Publish the results.

CONCLUSIONS

It appears that since 1910 the reasons for promoting naturally planted rights-of-way have changed in emphasis but not in content. Conceivably, this is because erosion control and lower maintenance costs are more tangible than aesthetics, social well-being, and regional identity to politicians and agency heads. And yet, some state programs, like Minnesota and Texas, have found a major part of their focus is in proclaiming their regional identity through their roadside vegetation.

Despite our advances in ecological knowledge, the greater availability of prairie propagules, and the increased enthusiasm of state transportation departments, the urgency for action that earlier proponents felt remains. In fact, it is even greater now than it was 60 or 80 years ago because then many of the roadsides were still in prairie and native shrubs. Commenting on this change, Aldo Leopold wrote

> Our grandfathers...killed off the prairie fauna and they drove the flora to a last refuge on railroad embankments and roadsides. To our engineers this flora is merely weeds and brush. Through processes of plant succession predictable by any botanist, the prairie garden becomes a refuge for quack grass.
>
> Leopold 1953

Naturalist May Watts tells a story that is a pertinent reminder to all advocates of the naturally landscaped roadside, past, present, and future:

> It so happens that while inspecting a new historical marker near Plainfield, Illinois, I met a local politician who said, "This, to me, is Illinois," as he stretched out his arm to the landscape. My eyes followed the arc of his gesture. "Illinois? Just exactly where?" Not the granite marker. That was Vermont. Not the expensive evergreen planting that had been hastily installed. That consisted of Mugo pine from the mountains of Switzerland. Not the big basket of garden flowers set at the base of the marker. The flowers were marigolds and zinnias and dahlias, whose ancestors all came to us from Mexico. Not the sparrow that alighted long enough to mark the marker. He was English. Not the freshly clipped grass at our feet. That was bluegrass from Eurasia. Not the weeds in the grass.
>
> Watts 1957

Today we are witnesses to, and participants in, the reversal of losses to our natural environment. This endeavor will take considerable energy, but should reap substantial rewards for ourselves and for future generations who will travel the pathways we leave for them.

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WILDFLOWER ROUTES: BENEFITS OF A MANAGEMENT PROGRAM FOR MINNESOTA RIGHT-OF-WAY PRAIRIES

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Abstract. Prairie once covered nearly 50% of Minnesota; however, it is rapidly becoming one of Minnesota's rarest native plant communities. In southeastern Minnesota, rights-of-way are essentially the only remaining areas where significant amounts of prairie still occur. The highway 56 right-of-way contains prairie that has been protected between the road and a now abandoned rail line. Since 1983, the prairie there has been managed jointly by the Minnesota Departments of Transportation and Natural Resources. Prescribed fire has nearly completely replaced herbicides and mowing as vegetation management tools. High species diversity has been maintained, and several populations of rare plants flourish under the new management program. In addition, the season-long scenic beauty of the prairie has enabled the Minnesota Department of Transportation to designate a portion of trunk highway 56 a "Wildflower Route." Because there are so many benefits—practical, economic, ecological, and aesthetic—the highway 56 management program is now being used as a model for the management of right-of-way prairies throughout Minnesota.

INTRODUCTION

In the past two years (1989, 1990), Minnesota has designated six wildflower routes. The designation of these routes is the culmination of many years of hard work and dedication by the Minnesota Departments of Transportation (Mn/DOT), Natural Resources (Mn/DNR), and Trade and Economic Development, as well as communities, private individuals, and conservation groups. This paper summarizes the findings of Bolin et al. (1990) and discusses in more detail the benefits of ecological management of prairie vegetation along roadsides, which has lead to increased interest in preserving and re-establishing prairie along Minnesota roadsides.

Prior to European settlement, the dominant vegetation community of the upper-midwestern United States was tallgrass prairie. However, since that time, large expanses of native vegetation (including prairie) have become increasingly less common. Nearly one-third of Minnesota was native prairie (Figure 1), but less than 1% of it is left (Wendt 1987). Much of the remaining native prairie is in areas that were unsuitable for agriculture, such as steep bluffs, cemeteries, and along rights-of-way.

Historically, rights-of-way have been recognized as refuges for native vegetation communities (Shimek 1925). This is particularly true in the shared rights-of-way of railroads and highways that were constructed through the tallgrass prairie region of North America. When the first railroads were built, prairie species re-established themselves in rights-of-way disturbed by construction. Subsequently, many highways were built adjacent to railroad tracks, and frequently, long narrow corridors of prairie were isolated and protected in the shared highway and railroad rights-of-way. These corridors were left undisturbed by agriculture, while the surrounding prairie disappeared. Periodic fires started by trains along railroad rights-of-way have enabled the fire-adapted prairie species to flourish (White 1986).

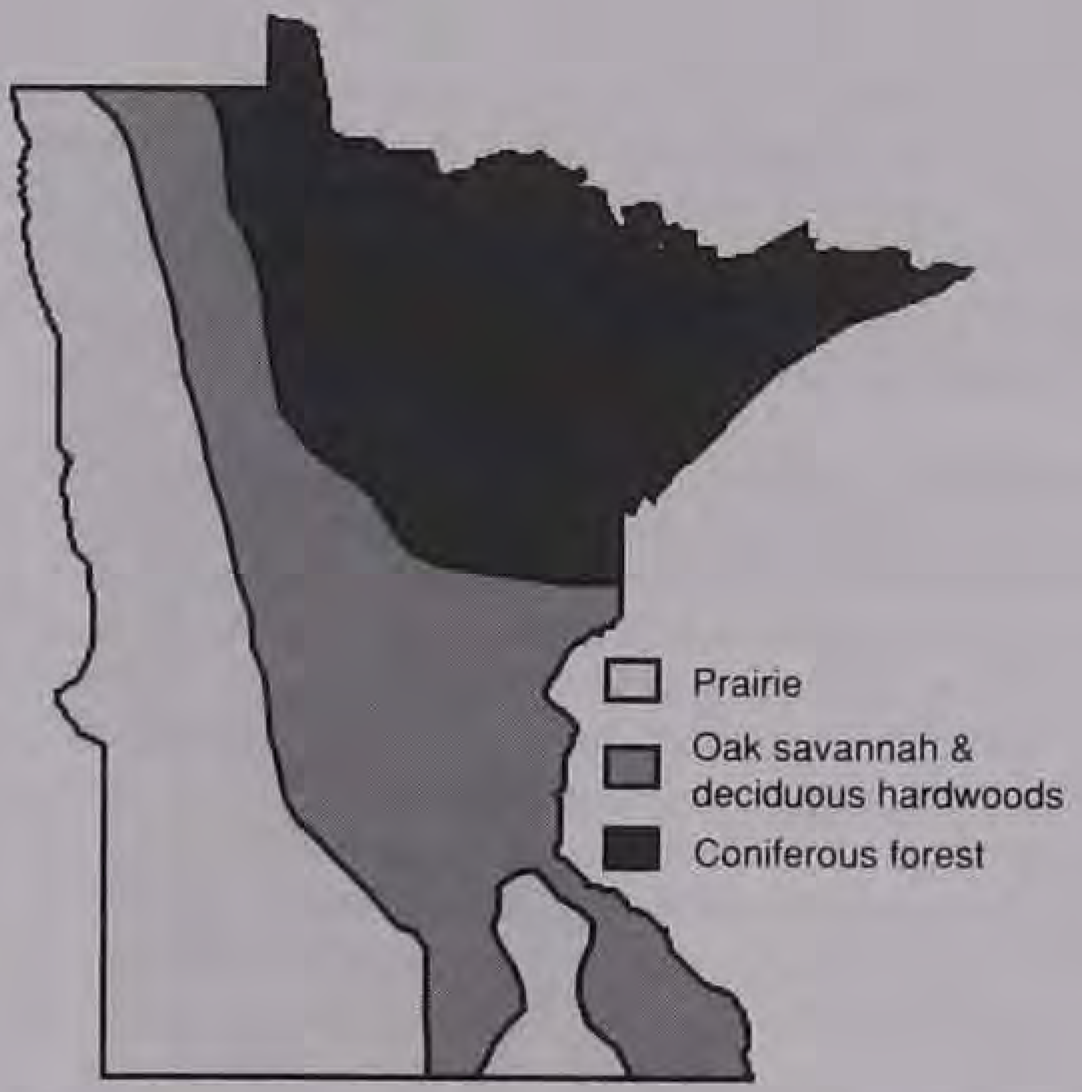

Figure 1. Major vegetation communities of Minnesota circa 1850s (Adapted from Moyle and Moyle 1977).

In 1978, The Nature Conservancy (TNC) and the Mn/DNR sponsored a vegetation survey of highway and railroad rights-of-way in central and western Minnesota. Results of this survey, published in 1983 (Borowske and Heitlinger 1983), identified sixteen corridors (544 miles) that contained high- to fair-quality native prairie species. Bolin et al. (1980) identified nine additional corridors in southeastern Minnesota that contained high-quality native prairie vegetation.

From 1988 to 1989, roadsides along the state highway system were surveyed for native plant communities by the Mn/DOT. It was found that about 50% of the right-of-way prairies identified in the late 1970s by Borowske and Heitlinger (1983) and by Bolin et al. (1980) had been destroyed. The survey also identified nearly 450 additional miles of high-quality prairie between state highways and railroad lines (Bolin et al. 1990). Species inventories indicated that the edges of the prairie remnants were disturbed and contained many non-prairie species, including noxious weeds. However, when compared with roadsides planted with introduced grasses and forbs (herbaceous species), roadsides containing prairie vegetation

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appeared to hold out undesirable species very well (Bolin et al. 1990). As a result of the survey, it was hypothesized that normal roadside management practices have kept roadsides in a cycle of disturbance that actually favors many undesirable species. It was also felt that roadsides containing prairie could be managed using a combination of traditional and non-traditional practices, and the disturbance cycle could be broken.

It is well known that fire had a major role in maintaining a balance between prairie and forest, and fire has been the tool of choice for the management of prairie preserves. Because of potential safety hazards, logistics, and a lack of training, highway departments have been slow to embrace the use of fire as a roadside management tool. However, in the past several years, Minnesota has demonstrated that burning can be performed effectively and safely along state highways where there is high traffic flow. Interagency cooperation involving the Mn/DOT and the Mn/DNR has allowed Minnesota to accomplish safe roadside burns.

The right-of-way along trunk highway 56 in southeastern Minnesota was one of the first identified to contain a prairie remnant. It is also the first right-of-way prairie remnant to be managed using prescribed burns, and now, fire has nearly replaced herbicides and mowing. Burns that favor prairie species have been timed to set back brush and non-native grasses. As a result, the native prairie community on the roadside has been stabilized, and the cycle of disturbance and weed infestation has been broken. Along highway 56, the decline in the prairie's health and vigor has been halted; high species diversity has been maintained; and several populations of rare plants continue to flourish under the new management program.

To increase public awareness of the value of roadside prairies, the highest quality corridors are designated as wildflower routes. Signs indicate the beginning of a route and also point out exceptional areas of prairie wildflowers. Route dedications include day-long activities, such as ribbon-cutting ceremonies, interpretive prairie tours, and activities arranged and coordinated by communities along the wildflower route. Prompted by the designation of highway 56 as a wildflower route, local communities have formed a coalition called "Prairie Visions" to utilize prairie as a natural resource in promoting tourism in southeastern Minnesota. Activities such as this have brought a heightened awareness of the natural and cultural value of prairie to the people of Minnesota.

METHODS

Vegetation Survey

The initial Mn/DOT vegetation survey was designed to locate remnant prairies as rapidly as possible. Once located, protection and management plans for the remnants are implemented, and more detailed inventories can follow. The presence of five or more prairie grasses, and certain forb species, served as an indicator of high-quality (A) prairie vegetation. Disturbed, or fair-quality prairie vegetation, was designated (B) and was characterized by having fewer than five prairie grasses or having a large number of non-native species present. Quality (C) indicated no prairie species were present (Bolin et al. 1990; Borowske and Heitlinger 1980). Highway rights-of-way were reviewed from a moving vehicle for indicator species. Stops were made periodically where indicator species were observed, and quality assessments were made. Occasionally, more detailed inventories were performed at sites that were determined to be quality A. Additional notes were taken relating the quality of the entire corridor to the sites surveyed.

Species Inventory

When conducted, a species inventory was performed along a stretch of roadside that was approximately one hundred feet long. The inslope, ditch bottom, backslope, and the railroad right-of-way were all included in the survey. All plants which were blooming and any identifiable species still in the vegetative stage were documented using a simplified version of Braun-Blanquet's Floristic System (Braun-Blanquet, 1965). This system identified the species present, along with their relative cover/abundance and sociability. The following additional information was also frequently recorded: site conditions (dry, mesic or wet); length and continuity of the native vegetation stand; adjacent land use; indications of disturbance by railroad, utility, or highway maintenance activities; presence of natural or constructed fire breaks (for future burn management); potential for extending the stand via restoration, and potential for harvesting seed from the site for future restoration purposes.

Preservation and Management of the Highway 56 Prairie

Bolin et al. (1980) initially identified highway 56 as containing a high diversity of prairie species. Since that time, it has been managed cooperatively by the Mn/DOT and the Mn/DNR. In 1983, highway 56 was posted with *Do Not Mow* and *Do Not Spray* signs so that maintenance personnel, utilities, and adjacent landowners did not mow, hay, or spray herbicides in the right-of-way. Permits allowing utility construction and herbicide use in the right-of-way have been closely monitored and have sometimes been restricted by the Mn/DOT Area Maintenance Engineer when it was deemed that their activities posed a threat to the prairie community. In addition, highway 56 has recently been posted with special *Wildflower Route* signs to notify the public that the highway is of special significance.

Also since 1983, parts of the highway 56 right-of-way have been managed using prescribed burns performed by crews composed of Mn/DOT and Mn/DNR personnel. A corridor management plan has been developed in which the right-of-way is divided into individual burn units, ranging from 0.25 to 0.5 miles in length, as determined by natural or constructed fire breaks. A fire prescription for each unit outlines burn parameters, including season, relative humidity, temperature, and wind direction, and the purpose of the burn. Management plan objectives, such as brush control, weed control, and prairie vegetation enhancement, are outlined in the corridor management plan. Fire breaks are placed around structures, such as utility poles, located in the right-of-way. Proposals are approved by the area Mn/DNR forester and/or the Pollution Control Agency. Local enforcement agents, fire departments, and adjacent landowners are also contacted. If the right-of-way is shared with a railroad or with private utility companies, their permission to perform the burn is also obtained.

During a burn, traffic is monitored by Mn/DOT personnel at all times, and the work areas are marked with *Roadwork Ahead* signs. If weather conditions fit those prescribed in the burn proposal, traffic is allowed to flow as usual. However, if the wind direction shifts, affecting visibility, then traffic is slowed or stopped, and a pilot car guides traffic through the work area. If traffic flow is stopped, waiting motorists are given information packets describing what the prescribed burns accomplish.

Prescribed burns are designed to accomplish several objectives: 1) stop the encroachment of brush into the prairie remnant; 2) decrease the abundance of cool-season, non-native grasses that are often present; and 3) enhance the growth of native, warm-season grasses and forbs. To accomplish these objectives, burns are performed in mid- to late May when the cool-season grasses are actively growing, and the native, warm-season grasses are still dormant. Qualitative assessments of burns are performed later in the season and again the following year. Individual segments are burned on a three- to five-year cycle.

RESULTS

The Mn/DOT vegetation surveys reviewed approximately 3,000 miles along 35 Minnesota highways for remnants of native vegetation communities (Table 1). These surveys included the highways surveyed by Borowske and Heitlinger (1978) and Bolin et al. (1980). Bolin et al. (1990) estimated that 30-50% of the quality A rights-of-way identified in 1978 and 1980 have been destroyed or degraded significantly (Figure 2, Table 2). The major causes for loss or degradation of native vegetation communities in rights-of-way are 1) abandonment of the rail-line by the railroad and subsequent reconveyance of the railroad right-of-way to adjacent landowners, who put the land to agricultural use; 2) highway reconstruction, repair, and maintenance activities; 3) utility and railroad maintenance activities; and 4) haying/mowing of rights-of-way by adjacent landowners. Approximately 15% (450 miles) of the 3,000 miles of highway right-of-way reviewed by the Mn/DOT contained quality-A native vegetation. Very few of the corridors had long continuous stretches of high-quality native vegetation. However, many corridors contained long, intermittent stretches of high-quality prairie vegetation.

Table 1. Community type and quality of rights-of-ways surveyed in 1988 and 1989.

Highway	*Community type*[a]	*Quality*
T.H. 1	P	A
T.H. 2[b]	NCF	B
T.H. 4	P	B
T.H. 6	NCF	B
T.H. 7	P	A (Intermittent)
T.H. 9[b]	P	A
T.H. 10[b]	P	A (Intermittent)
T.H. 11	P/DH	A
T.H. 13[b]	P	C
T.H. 14	P	A (Intermittent)
T.H. 22[b]	P	A (Intermittent)
T.H. 23[b]	P	B
T.H. 30	P	B
T.H. 32[b]	P	C
T.H. 34	NCF	B
T.H. 46	NCF	B
T.H. 52 (old)[b]	P	B
T.H. 53	NCF	B
T.H. 56[b]	P	A
T.H. 59	P	A (Intermittent)
T.H. 60	P	A
T.H. 61[b]	NCF	B
T.H. 65[b]	P	B
T.H. 71[b]	NCF	B
T.H. 72	NCF - bogs	B
T.H. 73	NCF	B
T.H. 75[b]	P	A (Intermittent)
T.H. 83	P	B
T.H. 89	NCF/DH	B
T.H. 102[b]	P	C
T.H. 169	NCF	C
T.H. 210	P/DH/NCF	B
T.H. 212	P	A (Intermittent)
T.H. 218[b]	P	A
T.H. 371[b]	P/DH/NCF	A (Intermittent)

[a] P = Prairie; DH = Deciduous Hardwood Forest; NCF = Northern Coniferous Forest.

[b] Previously Surveyed.

Rights-of-way that were considered to be quality A upon initial review were always found to contain a very high diversity of native species . Table 3 shows a species list for highway 56, a quality-A right-of-way, and Table 4 shows some of the indicator species used to determine the quality of a right-of-way. Native grasses served as the best criteria for gauging the quality of right-of-way vegetation. However, the presence of rare species or late-successional species, such as lead plant (*Amorpha* sp.) and pale purple coneflower (*Echinacea* sp.), also served as excellent indicators of high quality right-of-way. Many native forbs persist in areas dominated by disturbance indicator species, such as smooth brome (*Bromus inermis*), or they appear as volunteers in turf-planted roadsides. Many of the early successional composites—black-eyed susan, goldenrods and sunflowers—volunteer into brome-planted areas. Quality-B right-of-way vegetation was frequently found to be dominated by smooth brome with a few native forbs also present.

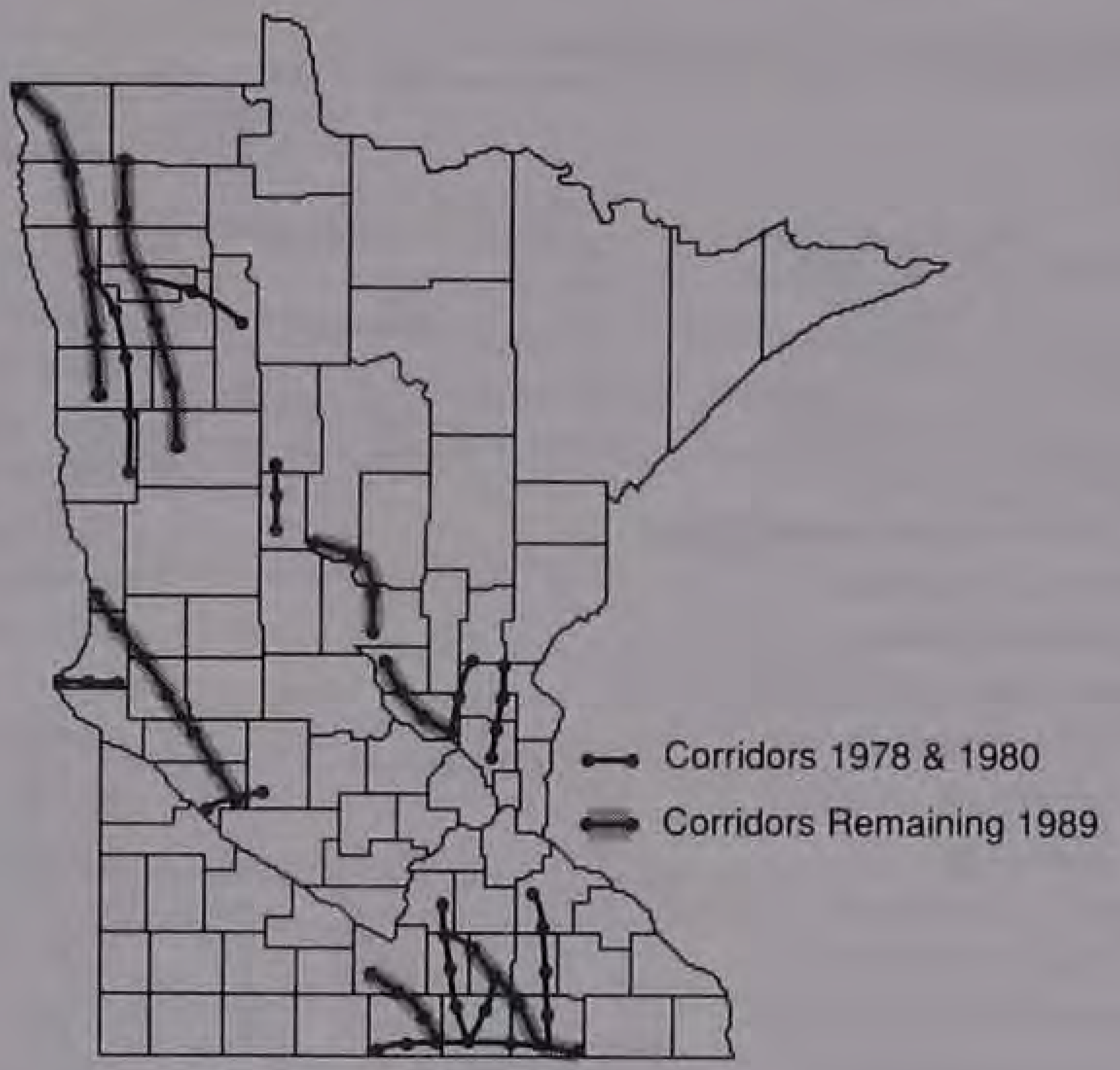

Figure 2. Prairie corridors lost since 1980.

Table 2. Change in quality of corridors from 1978 to present.

Highways surveyed 1988-1989	*Surveyed 1978*	*Surveyed 1980*	*D Quality*
T.H. 2	yes	no	Decline
T.H. 9	yes	no	No Change
T.H. 10	yes	no	Decline
T.H. 13	no	yes	Large Decline
T.H. 22	no	yes	No Change
T.H. 23	yes	no	Decline
T.H. 32[a]	yes	no	Large Decline
T.H. 52/56	no	yes	Large Decline
T.H. 56 (Mower Co.)[b]	no	yes	Improved
T.H. 61	yes	no	No Change
T.H. 65	no	yes	No Change
T.H. 71	yes	no	Decline
T.H. 75	yes	no	Decline
T.H. 102	yes	no	Large Decline
T.H. 218	no	yes	No Change
T.H. 371	yes	no	No Change

[a] Some sections in excellent condition

[b] On managed segments

In all rights-of-way surveyed, vegetation communities were in a state of flux. Native species were intermingled with non-native species that had been planted on the inslopes of the road bed or had invaded the right-of-way from adjacent fields. The highest-quality areas were generally found in ditch bottoms, backslopes, and in the railroad part of the shared right-of-way. The rights-of-way that contained native prairie grasses and wildflowers were rarely infested with noxious weeds, such as Canada thistle (*Cirsium arvense*) or leafy spurge (*Euphorbia esula*). When weeds such as these were observed in rights-of-way containing prairie species, they were generally in disturbed areas. Conversely, noxious weeds were frequently observed in smooth brome-dominated rights-of-way where the turf was declining in vigor due to drought stress or poor soil

Table 3. Highway 56 species list.

Grasses	
Andropogon gerardi	big bluestem
Elymus canadensis	Canada wild rye
Muhlenbergia sp.	unidentified muhly grass
Panicum virgatum	switch grass
Schizachyrium scoparium	little bluestem
Sorghastrum nutans	Indian grass
Spartina pectinata	prairie cordgrass
Sporobolis heterolepis	prairie dropseed
Stipa spartea	porcupine grass
Forbs	
Achillea millefolium	yarrow
Amorpha canescens	lead plant
Anemone canadensis	Canada anemone
Anemone cylindrica	thimbleweed
Artemesia ludoviciana	prairie sage
Asclepias incarnata	marsh milkweed
Asclepias speciosa	showy milkweed
Asclepias syrica	common milkweed
Aster ericoides	heath aster
Aster sp.	unidentified asters
Astragalus canadensis	Canada milk vetch
Baptisia sp.	unidentified indigo
Coreopsis palmata	stiff tick-seed
Cypripedium candidum	small white ladyslipper
Desmodium canadensis	Canada tic-trefoil
Dodecatheon media	shooting star
Eryngium yuccifolium	rattlesnake master
Fragaria virginiana	wild strawberry
Gallium boreale	northern bedstraw
Gentiana sp.	unidentified gentian
Geum Triflorum	prairie smoke
Helianthus grosseserratus	sawtooth sunflower
Helianthus rigida	stiff sunflower
Heliopsis helianthoides	common ox-eye
Iris virginica	blue-flag iris
Lespedeza capitata	round-headed bush clover
Liatris aspera	rough blazingstar
Liatris ligulistylis	meadow blazingstar
Liatris pycnostachya	gayfeather
Lilium michiganense	wood lily
Lilium philadelphicum	turk's cap lily
Lithospermum canescens	puccoon
Monarda fitulosa	wild bergamot
Oenothera biennis	evening primrose
Parthenium integrifolium	wild quinine
Petalostemum candidum	white prairie clover
Petalostemum purpureum	purple prairie clover
Phlox pilosa	prairie phlox
Platanthera praeclara	western prairie fringed orchid
Potentilla arguta	prairie cinquefoil
Psoralea argophylla	scurf pea
Pycnathemum virginianum	mountain mint
Quercus macrocarpa	bur oak
Ratibida pinnata	grey-headed coneflower
Rhus sp.	sumac
Rosa arkansana/setigera	wild rose
Rudbeckia hirta	black-eyed susan
Salix sp	willow
Sedge sp.	unidentified sedges
Silphium laciniata	compass plant
Sisyrinchium campestre	blue-eyed grass
Solidago missouriensis	Missouri goldenrod
Solidago rigida	stiff sunflower
Solidago sp.	unidentified goldenrods
Solidago speciosa	showy goldenrod
Spirea alba	meadow sweet
Thalictrum dasycarpum	meadowrue
Tradescantia occidentalis	spiderwort
Veronicastrum virginicum	Culver's root
Viccia americana	american vetch
Zizea aptera	heart-leaved alexander
Zizea aurea	golden alexander

conditions. Many rights-of-way contained turf-planted inslopes with established noxious weeds and prairie ditch bottoms and backslopes, which were noticeably less infested with noxious weeds.

The highway 56 right-of-way prairie community (Table 3) has flourished since the prescribed burn management plan was implemented by the Mn/DOT and the Mn/DNR in 1983. Fire management has reduced the encroachment of brush into the right-of-way, and the reduction in herbicide use and mowing has stimulated the native prairie species. Populations of two Minnesota rare species found along highway 56, rattlesnake master (*Eryngium yuccifolium*) and wild quinine (*Parthenium integrifolium*), have maintained or increased slightly in managed areas. Highway 56 also contains the only documented population of shooting star (*Dodecatheon media*) in Minnesota. The western prairie fringed orchid (*Platanthera praeclara*) has also been documented along highway 56 (Table 3).

DISCUSSION

The loss or degradation of 30-50% of the native vegetation corridors that were identified in 1978 and 1980, coupled with the overall decline of tallgrass prairie communities in Minnesota, has prompted state agencies and conservation groups to work together in identifying, preserving, and managing what remains of these plant communities in rights-of-ways. The methodology for identifying quality native vegetation communities in rights-of-way is rel-

Table 4. Some species of significance found in prairie rights-of-ways.

Native grasses - prairie indicators

- Big bluestem (*Andropogon gerardi*)
- Gramas (*Bouteloua* spp.)
- Switch grass (*Panicum virgatum*)
- Little bluestem (*Schizachyrium scoparium*)
- Indian grass (*Sorghastrum nutans*)
- Prairie cordgrass (*Spartina pectinata*)
- Dropseeds (*Sporobolis* spp.)
- Needle grasses (*Stipa* spp.)

Native forbs - prairie indicators

- Lead plant (*Amorpha* spp.)
- Blazingstars (*Liatris* spp.)
- Prairie clovers (*Petalostemum* spp.)
- Prairie phlox (*Phlox pilosa*)
- Purple coneflowers (*Echinacea* spp.)

Rare plant species

- Small white ladyslipper (*Cypripedium candidum*)[1]
- Rattlesnake master (*Eryngium yuccifolium*)[1]
- Prairie bush clover (*Lespedeza leptostachya*)[2]
- Wild quinine (*Parthenium integrifolium*)[1]
- Western prairie fringed orchid (*Platanthera praeclara*)[1]

Disturbance indicator species

- Quack grass (*Agropyron repens*)
- Smooth brome (*Bromus inermis*)
- Canada thistle (*Cirsium arvense*)
- Leafy spurge (*Euphorbia esula*)
- Sweet clover (*Melilotus officinalis*)
- Kentucky bluegrass (*Poa pratensis*)
- Timothy (*Phleum pratense*)

[1] Protected by the State of Minnesota.
[2] Protected by the Federal Government.

atively simple, but it does require botanical or ecological expertise. The preservation and management of these communities in rights-of-way requires the cooperation of all of the entities that utilize/share the right-of-way. The unique skills of personnel from both Highway Departments and Departments of Natural Resources are required to safely and effectively manage right-of-way native vegetation communities.

In summary, the Mn/DOT survey identified approximately 450 additional miles of right-of-way that contain high-quality native vegetation (Bolin et al. 1990). It is estimated that 80% of the areas identified contain native prairie grasses and wildflowers or a mix of prairie/deciduous hardwood forest plant species. All of the rights-of-way identified as containing high-quality native plant communities had a high diversity of species. Approximately an equal amount of lesser-quality prairie also occurs in Mn/DOT rights-of-way.

Nearly all of the rights-of-way identified had active or recently abandoned railroad lines adjacent to them. In many instances the highest-quality native vegetation was found in the railroad right-of-way; however, the ditch bottom and backslopes of Mn/DOT rights-of-way frequently contained high-quality native vegetation as well. Inslopes nearly always contained species comprising regular Mn/DOT turf mixes, the majority of which contain non-native grasses and legumes. The remnants identified were rarely continuous; they were generally broken up by disturbed or planted areas. Because trains frequently start fires which burn right-of-way vegetation, Bolin et al. (1990) hypothesized that the fire history of these areas has played a major role in the ability of the native vegetation communities to resist invasion by introduced, cool-season species and noxious weeds or, in the case of prairie, encroachment by woody species.

For practical purposes, vegetation along roadsides must be able to persist under frequently harsh conditions. It was apparent from the Mn/DOT survey that rights-of-way containing established native vegetation communities were less susceptible to drought-kill, weedy invasion, and erosion than were those rights-of-way that contained introduced species. With the management plan that has been implemented on the highway 56 right-of-way, the use of herbicides and mowing for weed control has decreased. Fire has reduced the need for chemical and mechanical removal of brush, as well. Under the present management plan emphasizing the enhancement of the native prairie community along highway 56, it is anticipated that the need for mowing will decrease to keeping the inslopes mowed short, the sight-lines clear for safety purposes, and patch mowing of weeds. This type of management decreases disturbance of the right-of-way substantially. Remaining natural disturbances are beyond our control, but native species are adapted to survive these.

Prairie grasses and wildflowers have more extensive root systems than traditional turf grasses and provide better soil holding capabilities in the long-term. The fact that they are adapted for Minnesota climate allows them to survive harsh winters and severe droughts, which take their toll on non-native turf grasses. In the long run, reduced herbicide use will save the state money and it will decrease the possibility of contaminating ground-water supplies. We also anticipate that a decrease in mowing will save the state money, and will increase the wildlife habitat value of roadsides.

The benefits of native vegetation on roadsides are many; whether it be preserving, managing and enhancing prairie remnants, or re-establishing native grasses and wildflowers on roadsides. In Minnesota, we feel that shifting from agronomic management practices, which rely primarily on herbicides and mowing, to more ecological practices, which incorporate prescribed burns, will bring about several things. We will break the cycle of constant disturbance of roadside vegetation that invariably leads to weed invasion, and more herbicide use and mowing. Instead, management to enhance and stabilize native vegetation communities will reduce disturbance and maintain favorable growing conditions for prairie species that compete favorably with weeds.

To further explore the possibilities and benefits in working with native vegetation on Minnesota roadsides, the Mn/DOT and the Mn/DNR have begun cooperation, on a state-wide basis, in developing an integrated roadside vegetation management program. An interagency committee has been formed to set guidelines for such a program. In the spring of 1990, the Mn/DOT sponsored several prescribed- burn training schools around the state. These schools combined the expertise of the Mn/DNR, University of Minnesota, U.S. Fish & Wildlife Service, and Mn/DOT personnel to train state personnel in prescribed burn techniques. Management to enhance native prairie communities, similar to that being used along highway 56, began along a number of Minnesota highways in 1990.

Six Wildflower Routes were designated in Minnesota between 1989 and 1990 (Figure 3). All of these routes are composed of remnant native plant communities, such as prairie. A pleasant surprise is that is that the local communities have become very involved in the promotion of these routes. They feel that posting and promoting Wildflower Routes may bring a resurgence of tourism to their areas. The financial benefit to regional tourism is as yet unrealized, but the potential appears to be excellent.

Wildflower Routes can mean many things to many different people—beautiful roadsides, enhanced wildlife habitat, less chemical use, preservation of a disappearing natural resource, native seed sources for future planting projects, lowered roadside maintenance costs, and the protection of rare features, such as endangered plants. The designation of six Wildflower Routes in Minnesota is testimony to the fact that the goals of the Department of Transportation, the Department of Natural Resources, and conservation groups can all be met; while at the same time, the travelling public benefits by seeing part of Minnesota's natural heritage flourishing once again along it's roadsides.

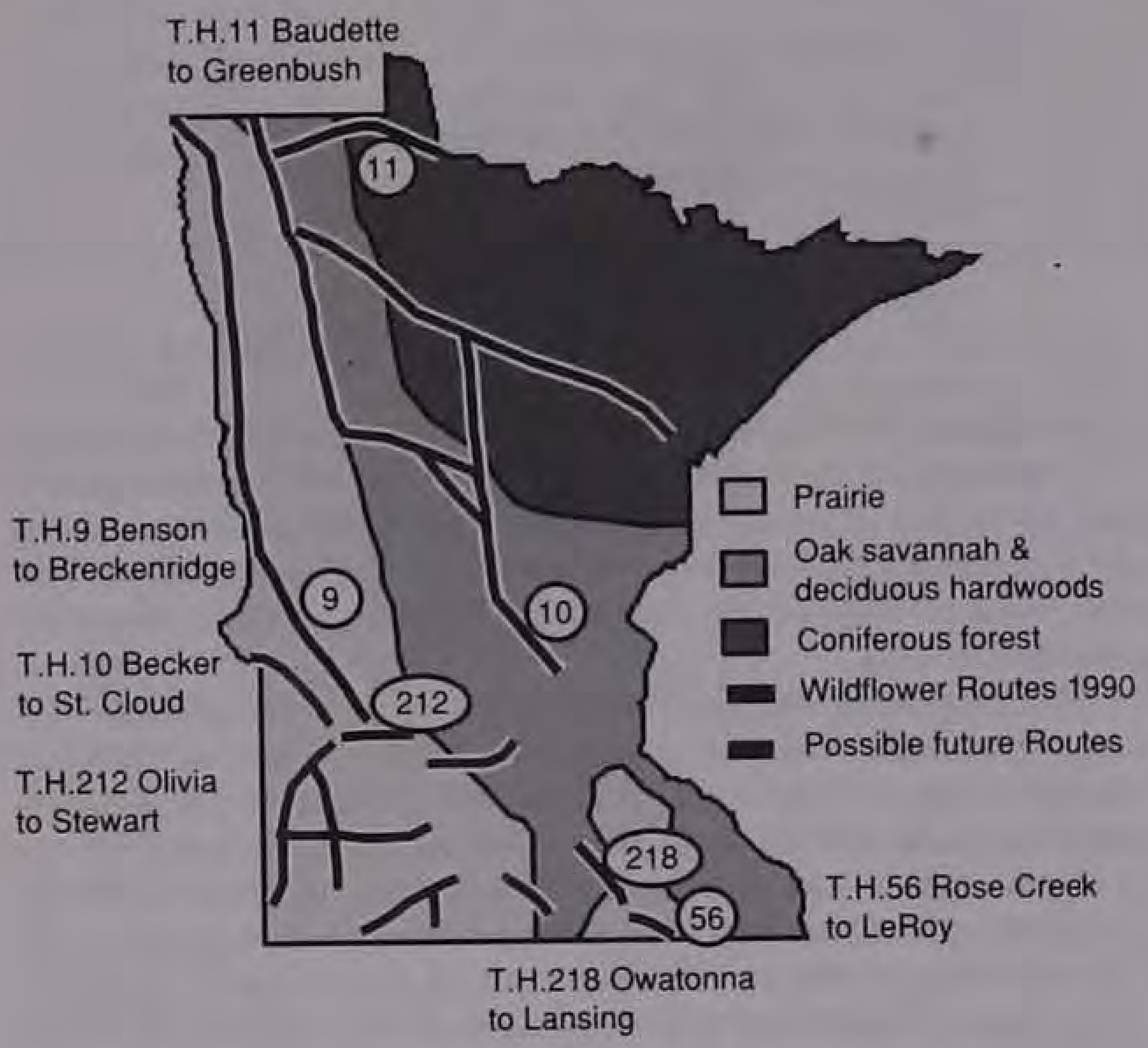

Figure 3. Minnesota wildflower routes.

ACKNOWLEDGEMENTS

The authors would like to acknowledge the efforts of the Minnesota Department of Natural Resources Roadsides For Wildlife Program and the Divisions of Parks and Recreation, Wildlife, and Forestry for their cooperation and assistance in implementing prescribed burn programs for Minnesota's Wildflower Routes.

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INTEGRATED ROADSIDE VEGETATION MANAGEMENT (IRVM): A COUNTY APPROACH TO ROADSIDE MANAGEMENT IN IOWA

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Abstract. Integrated Roadside Vegetation Management (IRVM) was started in Black Hawk County, Iowa, in 1985 as a new concept used on county rural roadsides. IRVM integrates native vegetation with appropriate management techniques to produce a roadside that is resistant to weed invasion and soil erosion, yet requires little or no maintenance. Following Black Hawk County's lead, many counties across Iowa have adopted IRVM techniques and hired County Roadside Managers to direct their roadside programs. Managers also work with rural landowners willing to use IRVM techniques on roadsides adjacent to their farmland. Today, this approach to roadside management is being implemented by state transportation departments across the upper Midwest and is attracting interest throughout the nation.

INTRODUCTION

Roadsides exist for a variety of reasons, but their primary function is to handle the concentrated flow of surface water from adjacent land and the road surface. Because of steep-sloping land and poor soil conditions within many roadsides, weed invasion and soil erosion are constant problems across Iowa. In 1985, a Roadside Vegetation Management Committee was established in Black Hawk County, Iowa, to address these problems. The committee concluded that the cause of weed invasion and persistence might not be marginal edaphic conditions, but rather the improper establishment and maintenance of Eurasian grasses and legumes. They proposed the establishment of native prairie vegetation in roadsides, and the integration of various vegetation management techniques to maintain the plant community, hence the name, Integrated Roadside Vegetation Management, or IRVM.

PROGRAM DESCRIPTION

The primary objective of IRVM is to establish and maintain a safe, stable, low-maintenance roadside that is attractive and healthy for all life. Whenever and wherever possible, native prairie grasses and wildflowers are used to fulfill this objective. Since 1985, twenty-three counties across Iowa have implemented an integrated approach to prevent weeds and control soil erosion in their roadsides. The Iowa Department of Transportation and transportation departments in Wisconsin, Minnesota, Nebraska, and Missouri are using similar programs in managing roadsides on their state and federal highways.

Instead of the traditional practice of seeding new or regraded rural roadsides with non-native smooth brome, *Bromus inermis* Leysser; Kentucky 31 tall fescue, (*Festuca arundinacea* Schreber; or Kentucky bluegrass, *Poa pratensis* Linnaeus, IRVM counties are using a mixture of five to seven native prairie grasses and an equal number of native prairie forbs. Native Iowa prairie vegetation has been shown to prevent the invasion of perennial and annual weeds while reducing woody species encroachment (Landers 1970). A diverse community of prairie grasses and forbs will also reduce surface runoff within the roadside, thus, reducing the chance for damaging soil movement and resultant gullies or siltation.

Counties utilizing an integrated approach to roadside management hire a professional roadside manager or biologist to oversee roadside activities. Commonly called County Roadside Managers, these employees are responsible for all facets of their county's integrated roadside program. In addition to seeding and maintaining rural roadsides with prairie grasses and forbs, they develop and implement annual and long-range, roadside management plans.

Roadside managers use various vegetation management techniques to maintain a vigorous stand on both prairie and non-prairie, rural roadsides to prevent weed invasion and control soil movement. A roadside burn every three to five years will increase native plant diversity, recycle nutrients, and retard the growth of any non-native, competing vegetation. The roadside-burn season typically begins in late April and lasts until mid- or late June. To maintain traffic safety, special burn equipment and crews are used, and extra precautions are taken. Established, perennial weeds are eradicated with one or more spot applications of a selected herbicide. After weeds are eliminated, the site is reseeded with a mixture of native prairie seed. Periodic mowing of road shoulders and dangerous intersections may be necessary to maintain traffic safety and allow adequate vehicular sight distance. As part of the roadside planning process, all management techniques are used carefully and later evaluated by County Roadside Managers.

In addition to weed prevention and soil erosion control, the use of native prairie vegetation also provides excellent wildlife habitat along Iowa's 228,000 ha of rural roadside. Rural roadsides with well-developed prairie will create corridors allowing native wildlife to move from one natural area to another. Also, Iowa travelers will experience the diverse vegetation, beauty, and scenic grandeur that greeted early settlers as they entered Iowa more than a century ago.

One aspect of Iowa's County Roadside Program that separates it from other state roadside programs is the emphasis on working with the local landowners. In Iowa, most of the land in county roadsides is owned by the adjacent landowner, but responsibility for roadside maintenance remains with the County Engineer or County Roadside Manager's office. County Roadside Managers spend considerable time talking to and working with rural landowners. In some cases, the landowners may already be involved with managing their own roadsides. It is not unusual to witness landowners spraying weeds or mowing grass in the roadside adjacent to their cropland, and 3-5% of the rural landowners in Iowa burn their roadsides in the early spring. However, many landowners do not use proper management techniques for roadside vegetation. Often, the grass is mowed too short and too frequently; herbicides are sprayed in the roadside as if it were a field of corn or soybeans; or roadsides are burned at the wrong time, with little or no fire safety equipment. In these situations, the County Roadside Manager contacts the rural landowner, explains the integrated approach to roadside management, and guides the landowner through the proper timing and use of roadside management techniques.

In other cases, a rural landowner may have a fairly good stand of native vegetation already existing in the county roadside. The County Roadside Manager will conduct a follow-up visit with the landowner to explain the integrated roadside program and possibly volunteer to manage the roadside. Regardless of the situation, County Roadside Managers are striving to work with landowners in their county.

FUTURE PROSPECTS

As counties use an IRVM program on their roadsides, they realize that traditional high maintenance and high costs are not necessary. Once established, Iowa's native prairie vegetation has proven to be effective in weed prevention and soil erosion control. County Roadside Managers, using appropriate management techniques, can maintain roadside vegetation while providing wildlife with excellent habitat and travellers, a colorful and scenic drive.

As IRVM gains in popularity across Iowa, County Roadside Managers are finding new challenges and asking more questions. For instance, solutions need to be found for temporary soil erosion that occurs while the native vegetation becomes established; the best formulas for prairie seed mixes and seeding rates need to be determined for specific roadside sites; the use of widely available cultivars of warm-season forage grasses needs to be compared to limited, locally grown native prairie seed; and many more. Those who support IRVM and promote the use of prairie species in roadsides can provide valuable assistance as questions and challenges surface and as new research needs to be done.

The forecast for the future of IRVM is favorable. Daily, an increasing number of county, state, and federal roadsides are being protected and managed with IRVM techniques. More County Roadside Managers are being hired. They, in turn, involve more landowners, interested individuals, and agencies in Integrated Roadside Vegetation Management.

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THE ROLE OF PRAIRIE ROAD BORDERS AS REFUGIA FOR HERBACEOUS PLANTS IN THE CENTRAL FLINT HILLS GRAZING REGION OF KANSAS

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Abstract. Remnants of native prairie vegetation, undisturbed by grazing cattle, remain along fenced county roadsides, forming a loose network throughout the Flint Hills of Kansas. The role of these roadsides as refugia in four centrally located counties was examined by comparing the composition and density of the roadside flora with the adjacent pastures. At each of 16 sites, paired quadrats (1 m x 10 m) were established parallel to the fence line. The number of stems bearing an inflorescence was recorded for each species, semi-monthly from May through September 1989. Species of roadside borders and adjacent grazed pastures can be grouped in five distinct categories: refuge-dependent species, refuge-benefited species, refuge-neutral species, refuge-independent species, and species of the immediate road edge.

INTRODUCTION

The herbaceous plants of the tallgrass pastures of the Kansas Flint Hills have supplemented the graminoid forage of large herbivores for millennia. Bison, pronghorn, elk, and deer utilized many herbaceous species during their feeding forays. Infrequent removal of foliage, flowers, and seeds by foraging animals allowed for vigorous regrowth from rootstocks. Species poorly adapted to grazing stress may have persisted in the flora.

The entry of domestic cattle into the area in the 1870s was followed by fencing of the range into units. With restricted movement, grazing pressure on herbaceous plants increased throughout the grazing season. The frequent removal of foliage and reproductive parts disrupted reproductive processes and reduced starch reserves in the perennial root systems. During the modern grazing history of the region, there has been an apparent reduction in diversity and density of these native herbaceous species (Stoddart et al. 1975).

Remnants of the native vegetation, undisturbed by grazing cattle, remain along fenced county roadsides, forming a loose network throughout the Flint Hills grazing region. In the current scientific literature, I found no studies of the role of roadside refugia in the ecology of the prairie ecosystem. In this study, the role of fenced road borders as refugia for native herbaceous plants was assessed in Chase, Lyon, Morris, and Waubaunsee counties in the central Flint Hills.

METHODS

Fenced roadsides and adjacent grazed pastures were compared at four sites in each county. Sites were located in native prairie areas where fenced roadsides were undisturbed by mowing or spraying and were adjacent to grazed pastures determined to be in good range condition. In each county, two sites were located on loamy upland or limey upland soils, and two sites were located on loamy lowland soils at the bases of hills or on terraces above intermittent streams. At each site, paired and opposite quadrats (1 m x 10 m) were established parallel to the fence line. Roadside quadrats were placed no less than 1/2 m from the fence, and the pasture quadrats were aligned within 5 m of the separating fence. On the upland sites, one quadrat pair was located on the north-facing slope and the other quadrat pair on the south facing slope.

Quadrats were visited at two week intervals from 1 May to 15 August 1989. Each species of herbaceous plant in flower was noted, and the number of stems bearing an inflorescence was recorded for each species. Counts of flowering stems for each species were totaled for refuge quadrats and for pasture quadrats during the 3 1/2 month period. The t test was used to determine the significance of differences between the data sets. Sources used for the identification and classification of the taxa encountered were works by Bare (1979) and Barkley (1968).

DISCUSSION

Data on species composition and counts of flowering stems from the quadrats revealed the floras of roadsides and pastures are distinctively different.

Five categories of species were determined by comparing border refuges and grazed pastures:

1. *Refuge-dependent species.* Their occurrence in grazed pastures was rare (Table 1).
2. *Refuge-benefited species.* These species showed significantly higher numbers (at the 95% confidence level) of flowering stems in the refuge quadrats than in the grazed pasture quadrats (Table 2).
3. *Refuge-neutral species.* Species in this category showed no significant differences in numbers (at the 95% confidence level) of flowering stems in the roadside borders when compared to the grazed pastures (Table 3).
4. *Refuge-independent species.* Most were herbaceous annuals with significantly higher numbers (at the 95% confidence level) of flowering stems in the grazed pasture quadrats than in the quadrats of the roadside refugia (Table 4).
5. *Species of the road edge.* This category was comprised of many annuals associated with disturbed soil of the road edge (Table 5). Plants in this category appeared in margins of quadrats that extended beyond border vegetation into the road edges.

Table 1. Refuge-dependent species.

	Sum of flower-bearing stems	
Species	*Border refugia*	*Grazed pastures*
Desmanthus illinoensis (Michx.) Mac. M.	293	4
Echinacea angustifolia D.C.	218	11
Silphium laciniatum L.	215	2
Helianthus maximiliana Schrad.[1]	196	4
Silphium speciosum Nutt.	177	0
Cassia fasciculata Michx.	128	0
Helianthus tuberosa L.	101	1
Euphorbia corollata L.	85	2
Oenothera macrocarpa Nutt.	44	2
Petalostemum multiflorus (Nutt.)	33	2

[1] Counts from stems with swollen flower buds.

Table 2. Refuge-benefited species.

	Sum of flower-bearing stems	
Species	*Border refugia*	*Grazed pastures*
Fragaria virginiana Duchesne	488	63
Asclepias tuberosa L.	336	42
Oxalis dillenii Jacq.272	53	
Rudbeckia hirta L.	257	5
Petalostemum purpureum (Vent.)	226	48
Viola pedata L.	210	41
Viola practinocola Greene	208	38
Tradescantia bracteata Small	196	3
Schrankia nuttallii (D.C.) Standl.	181	24
Petalostemum candidum (Willd.) Michx.	175	20
Penstemon cobaea Nutt.	144	31
Anemone caroliniana Walt.	110	29
Linum pratense (Nort.) Small	107	26
Antennaria neglecta Greene	97	32
Gaura parviflora Dougl.	96	17
Liatris punctata Hook	88	15
Allium canadense L.	86	19
Asclepias verticillata L.	71	11
Polytaenia nuttallii D.C.	59	14
Lespedeza capitata Michx.	51	16
Teucrium canadens L.	50	10
Lithospernum incisum Lehm.	41	8
Monarda citriodora Cerv.	30	6
Hedyotis crassifolia Ref.	22	5
Liatris pycnostachya Michx.	17	7
Cacalia tuberosa Nutt.	11	5
Ratibida columnifera (Nutt.) (Wooton & Standl.)	4	1

Table 3. Refuge-neutral species.

	Sum of flower-bearing stems	
Species	*Border refugia*	*Grazed pastures*
Solidago missouriensis Nutt.	248	215
Amorpha canescens Pursh	192	177
Senecio plattensis Nutt.	163	156
Psorelea tenuiflora Pursh	160	176
Helianthus scalicifolius A. Dietr.	144	138
Sisrinchium campestre Bickn.	112	128
Achillea lanulosa L.	111	117
Astragalus crassicarpus Nutt.	80	94
Oxalis stricta L.	73	67
Tragopogon dubius Scop.	72	75
Baptisia leucophaea Nutt.	71	78
Baptisia australis (L.) R. Br.	64	63
Nothoscordum bivale (L.) Britt.	55	46
Solidago ridiga L.	48	43
Delphinium virescens Nutt.	43	47
Oxalis violacea L.	41	48
Lomatium foeniculaceum (Nutt.) T. & G.	18	14
Ruellia humilis Nutt.	11	13
Hypoxis hirsuta (L.) Coville	7	7
Verbena canadensis (L.) Britt.	9	8
Corydalis crystallina Engelm.	6	8

Table 4. Refuge-independent species.

	Sum of flower-bearing stems	
Species	*Border refugia*	*Grazed pastures*
Xanthocephalum dracunculoides (D.C.) Shinners	4	81
Vernonia baldwini Torr.	0	42
Euphorbia marginata Pursh	1	40
Ambrosia psilostachya D.C.	1	37
Artemesia ludoviciana Nutt.	2	26
Erigeron strigosus Muhl.	1	23
Cirsium undulatum (Nutt.) Spreng.	1	8
Opuntia polyacantha Haw.	1	6

Table 5. Disturbed-road-edge species.

	Sum of flower-bearing stems	
Species	*Border refugia*	*Grazed pastures*
Melilotus officinalis (L.) Lam.[1]	304	32
Melilotus alba Desr.[1]	128	21
Solanum rostratum Dunal.[1]	174	11
Kochia scoparia (L.) Schrader[1]	179	10
Thlaspi arvense L.[1]	169	16
Erysimum repandum L.[1]	160	14
Oenothera speciosa Nutt.	156	11
Conyza canadensis (L.) Cronquist	113	6
Chrysanthemum leucanthemum L.[1]	112	12
Polygonum pennsylvanicum L.	106	12
Verbascum thapus L.[1]	102	11
Cichorium intybus L.[1]	95	10
Rumex crispus L.[1]	67	3
Verbena stricta Vent	64	7
Saponaria officinalis L.[1]	33	2
Apocynum cannabinum L.	18	1
Ambrosia trifida L.	12	2

[1] Introduced species.

Species in the refuge-dependent category are unable to tolerate prolonged grazing. Low tolerance to soil compaction, a condition often associated with grazed pastures, may have contributed to their decline. Vigorous populations in the roadside borders were abruptly absent within grazed areas. After extensive searches away from the quadrat sites, only occasional, widely scattered plants were found in grazed areas. These refuge-dependent species represent the plant families of Asteraceae, Fabaceae, Euphorbiaceae, and Onagraceae. These species are major contributors to the aesthetics of prairie roadways.

Refuge-benefited species were more tolerant of grazing than the refuge-dependent taxa, but numbers of flowering stems were sharply reduced in the pasture quadrats compared to the roadside refugia. Reduction of flowering stems in grazed pastures was a function of lower plant densities per unit area and reduced vigor of surviving plants. These refuge-benefited species could decrease in number and vigor if the range condition were allowed to deteriorate from good to fair. Proper stocking rates were vital to the survival of the species in this category of herbaceous perennials.

Refuge-neutral species remained in the prairie flora because of adaptations which allowed them to avoid excessive foliage removal by grazing animals. Many of these herbaceous species gained protection through low palatability due to unpleasant textures, flavors, or toxic compounds. Others avoided grazing by emergence and anthesis in the prevernal period, prior to the grazing season.

Refuge-independent species were rare or absent in the roadside borders but were found in grazed pasture quadrats where water erosion scars or cow paths reduced the native vegetation cover. These invaders were primarily herbaceous annuals of low forage value.

Disturbed-road-edge species were less successful in establishing in grazed pastures than were the refuge-dependent species but invaded pastures if they were severely overgrazed by livestock. This group, dominated by species of annuals introduced from Eurasia, presents no immediate threat to the integrity of well-managed grazing lands, but they do add diversity to the grassland flora.

This study suggests that roadside borders are refugia for prairie plants. These linear preserves contain plant assemblages valuable for comparison with adjacent ranges impacted by decades of cattle grazing. Management to maintain and enhance prairie elements is encouraged: timely burning to remove invading woody plants, reduction or elimination of the use of herbicides, and mowing along roadways. This study suggests that grazing has a negative impact on prairie species. Therefore, construction and maintenance of quality fences along prairie roads are encouraged to prevent entry of livestock into the border vegetation. Public education to enhance appreciation of the aesthetic and ecological values of the floral diversity of prairie road borders is also necessary to support this type of management program. This study of roadside borders and grazed pastures has provided insights into changes in the tallgrass prairie vegetation as a result of intensive livestock grazing. Additional scientific studies of the microenvironment of prairie road borders and the ecological dynamics of the floral complex are needed to prepare strategies for future management.

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B.A. Seger

RELATIONSHIP OF ADJACENT LAND USE TO ROADSIDE PRAIRIE GRASS OCCURRENCE IN LEE COUNTY, IOWA

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Abstract. Adjacent land use and native grass occurrence were recorded for 13,833, 0.16-km increments of roadside during 1988. Frequency distributions of three native grass species differed significantly from expected ($P <$ .005). Calculation of expected values was based upon adjacent land use proportions. Occurrence of Indian grass *Sorghastrum nutans* (L.) Nash and switchgrass, *Panicum virgatum* L., was less than expected adjacent to cropland (50% and 49% versus 55% expected) and greater than expected adjoining woodland (20% and 19% versus 14%, $P < .05$). Canada wildrye, *Elymus canadensis* L., occurrence was less than expected adjoining pasture (18% versus 20%) and greater than expected adjacent to woodland (17% versus 14%, $P < .05$). Relationships for big bluestem, *Andropogon gerardi* Vitman, and tall dropseed, *Sporobolus asper* (Michx.) Kunth, were not significant. Soil disturbance reflected land-use intensity and helped explain occurrence of native grasses in roadsides. Woodlands with histories of low land-use intensity may harbor prairie remnants and, thus, serve as native-grass refugia to recolonize roadsides. Efficient identification of roadsides with remnant prairies may be achieved by focusing initial efforts on areas such as woodlands, which lack intensive land-use histories.

INTRODUCTION

Identification of roadside prairie remnants is important for the increasing number of right-of-way vegetation management programs that feature native grasses and wildflowers. For example, county and state programs in Iowa and state programs in Minnesota and Wisconsin emphasize native plants. Three tasks applicable to the initiation of such prairie roadside programs are 1) a roadside inventory to identify the location and condition of native prairie remnants, 2) a prescribed burning program to reinvigorate native remnants, and 3) demonstrations of the public benefits of healthy roadside prairie.

In 1988, Lee County began the sixth integrated county roadside management program in Iowa. Inventory records were compiled in a data base that was used to identify roadside characteristics and set priorities for application of management practices such as prescribed burning. Once identified, selected roadside prairie remnants were burned to demonstrate the utility of prairie in roadside maintenance.

Previous prairie remnant inventories have frequently focused on soil surveys or railroad rights-of-way. County soil surveys have been used to identify prairie remnants by locating soil types of low utility for agriculture (Alverson 1990). The association of prairies and railroad rights-of-way has been investigated in Iowa by Braband (1986), in Illinois by Bacone and Harty (1981), and in Min-

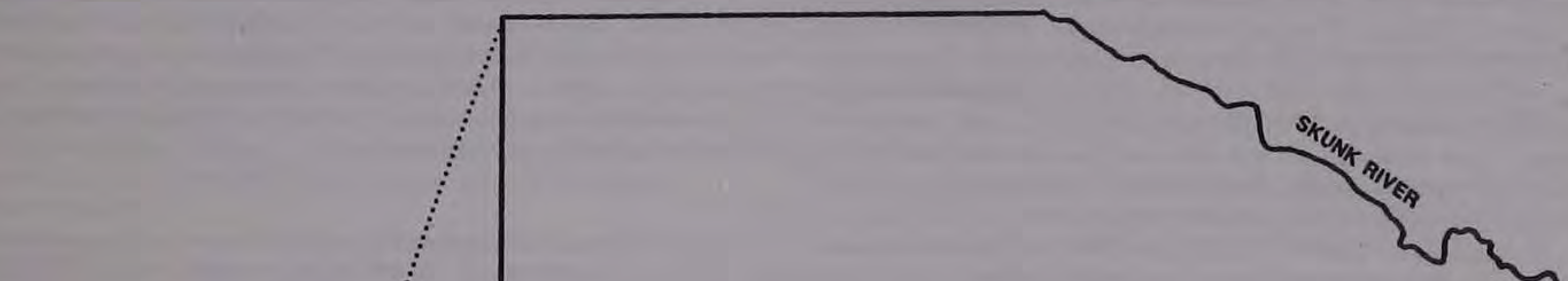

Figure 1. Location of Lee County in Iowa.

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[1] Current Address: Westwood Professional Services, Inc., 14180 Trunk Highway 5, Eden Prairie, Minnesota 55344

nesota by Borowske and Heitlinger (1983).

However, I found no reports in the literature that examined the relationship between adjacent land use and roadside prairie grass occurrence. Thus, this became an application of the computerized Lee County roadside inventory.

My principal objective was to determine if roadside occurrence of native grasses was influenced by adjacent land use. The null hypothesis was that distribution of native grass species in roadsides was independent of adjacent land use. If the hypothesis was true, then each species of native grass would have been distributed proportionately among adjacent land-use types.

STUDY AREA AND METHODS

Lee County, located in the southeast corner of Iowa, is bounded on three of five sides by the Mississippi, Des Moines, and Skunk rivers (Figure 1). The county land base is approximately 15% forested, 15% developed for commercial and residential use, and 70% agricultural and range land. The western portion of the county includes part of Shimek State Forest, the largest contiguous state-owned forest tract in Iowa. Topography ranges from quite level in agricultural areas to hills divided by drainages in forested areas. The county maintains roughly 1,126 km (700 mi) of roads, ranging from paved farm-to-market roads to low maintenance roads. Because of the extensive drainage system within the county, dead-end and diagonal or crooked roads are frequent.

During 29 August through 12 October 1988, roadside characteristics were recorded for 13,833, 0.16-km (0.1-mile) increments of roadside bordering 1,113 km of road. Presence or absence of six native grass species was recorded for each increment of roadside. Native grasses included big bluestem, *Andropogon gerardi* Vitman; Canada wildrye, *Elymus canadensis* L.; Indian grass *Sorghastrum nutans* (L.) Nash; little bluestem, *Andropogon scoparius* Michx.; switchgrass, *Panicum virgatum* L.; and tall dropseed *Sporobolus asper* (Michx.) Kunth. Little bluestem was later dropped from the analysis because it occurred in only 1.7% of the roadside increments. Rural adjacent land use was classified into four categories: cropland, hayfields, pasture, and woodland. Residential and commercial land uses were excluded from the analysis

The location of each increment was coded on forms using the road-numbering system applied by the County Engineer's office to refer to roadsign locations. North-south roads were designated by odd numbers; east-west roads were indicated by even numbers. Roads were numbered consecutively from the northwest toward the southeast corner of each township. Each road number was preceded by a two-letter abbreviation of the township name.

Data were collected by two-person teams driving county roads in pickup trucks at approximately 16 km (10 mi) per-hour. Each team averaged 16-22 km (10-14 mi) per day. Data were gathered when native grasses were in seed and most detectable. Summer wildflowers, however, were inevitably somewhat overlooked because dry seed heads were less detectable than active blossoms. Inventory records were entered into a computerized data base, and the distribution of five species of native grasses among four types of adjacent land use was examined with chi square goodness-of-fit tests (Neu et al. 1974, Byers et al. 1984). Simultaneous confidence intervals (Byers et al. 1984) were used to determine if the observed proportional occurrence of each species adjacent to each land use was significantly different from expected.

RESULTS

Tall dropseed and Canada wildrye were the most common and most widely distributed native grasses in county roadsides. Together, they accounted for 73.3% of all native grasses in frequency counts (Table 1). Big bluestem, Indian grass, and switchgrass together accounted for 23.9% of the total native grass frequency. Little bluestem was excluded from analysis because it made up only 2.8% of the total frequency and occurred in only 1.7% of the roadside inventory samples. Overall, 48.2% of the 13,833 samples included at least one native grass species.

Relative frequencies of four adjacent land-use types ranged from 54.9% for cropland to 10.9% for hayfield (Table 2). Developed commercial and residential land uses composed less than 5% of the total inventory and were excluded from analysis.

Chi square tests indicated that distributions of Indian grass, switchgrass, and Canada wildrye were significantly different from expected ($P < .005$). These three species were not distributed proportionately among the four predominant land-use types (Table 3). Proportions of each species' distribution occurring adjacent to each land use was then tested with confidence intervals. Proportions of Indian grass and switchgrass adjacent to cropland (primarily corn) were less than expected, whereas these species occurred more frequently than expected in roadsides adjoining woodland ($P < .05$, Table 4). Additionally, Indian grass occurred less frequently than expected in roadsides adjacent to hayfields. Canada wildrye occurred less frequently than expected adjacent to pasture and more frequently than expected adjacent to woodland ($P < .05$).

Distributions of big bluestem and tall dropseed were not significantly different from expected. Tall dropseed was distributed quite evenly among land uses and occurred frequently in association with Kentucky bluegrass, *Poa pretensis* L. With the exception of hayfields, big bluestem reflected the general relationship exhibited by Indian grass and switchgrass, demonstrating a tendency toward increasing frequency with decreasing roadside disturbance level (Figure 2).

The geographic distribution of tall, warm-season grasses (switchgrass, Indian grass, and big bluestem) was related to land-use patterns within the county. Overall, these species occurred in 12.9% of the roadsides. Where adjacent land use was classified as woodland, these grasses occurred in 17.7% of the roadsides. Although tests were not significant for big bluestem, all three tall, warm-season species were generally more common in the western portion of the county and in particular near Shimek State Forest, where woodland was well represented.

Table 1. Frequency of six native grass species in 13,833, 0.16-km roadside inventory samples in Lee County, Iowa, 1988.

Species	*Frequency of occurrence*	*Percent frequency*	*Relative frequency*
Big bluestem	821	5.9	9.6
Canada wildrye	2,368	17.1	27.7
Indiangrass	652	4.7	7.6
Little bluestem	240	1.7	2.8
Switchgrass	576	4.2	6.7
Tall dropseed	3,904	28.2	45.6
All grasses, pooled	6,667	48.2	
Total	8,561		100.0

Table 2. Frequency of four land-use types adjoining 13,146[a] 0.16-km increments of Lee County roadsides.

Land use	*Frequency of occurrence*	*Relative frequency*
Cropland	7,214	54.9
Hayfield	1,437	10.9
Pasture	2,652	20.2
Woodland	1,843	14.2
Total	13,146	100.0

[a] 687 increments with developed land uses were excluded from the total.

Table 3. Chi square goodness-of-fit test on the distribution of five native grass species in roadsides, as related to adjacent land use in Lee County, Iowa.

		Frequency of occurrence									
		Big bluestem		*Canada wildrye*		*Indian grass*		*Switchgrass*		*Tall dropseed*	
Land use	*Percent of land use*	*Obs.*[a]	*Exp.*[b]	*Obs.*	*Exp.*	*Obs.*	*Exp.*	*Obs.*	*Exp.*	*Obs.*	*Exp.*
Cropland	54.9	432	463	1,300	1,314	334	367	275	307	2,248	2,216
Hayfield	10.9	93	92	262	262	55	73	59	61	420	441
Pasture	20.2	183	170	423	483	148	135	117	113	835	814
Woodland	14.0	136	118	410	36	132	4	109	79	534	566
Total	100.0	844		2,395		669		560		4,037	
X^2		5.71		31.35		24.02		15.47		3.81	
P		> .1		< .005		< .005		< .005		.1	

[a] Observed frequency.

[b] Expected frequency.

DISCUSSION

The distribution of native grasses in roadsides can be explained by a variety of factors, including soil disturbance, land-use intensity, and the successional niche of each grass species. Persistence of native grasses in roadsides adjoining woodlands reflects the less intensive land-use history of woodlands in comparison to cropland. Intensive land use that results in frequent disturbance or turning of the soil precludes most areas from serving as reservoirs of native grasses available for natural reestablishment of prairie roadsides. Agricultural fields where farmers fall-plowed close to or beyond the edge of roadsides ranked among the most intensive land uses and caused roadside disturbance. These disturbed roadsides were subsequently exposed to erosion and sedimentation during winter, producing a favorable environment for invasion of annual weeds. Roadsides that are subject to siltation must also be cleaned out periodically to perpetuate drainage. This ditch cleaning introduces another set-back to the natural successional process and native grass establishment.

The role of native grass species in plant succession is linked to their distribution in roadsides in relation to adjacent land use. Switchgrass and Indian grass do not typically reinvade fields or roadsides soon after disturbance, and their occurrence was negatively associated with land-use intensity. Tall dropseed, which establishes relatively soon after disturbance and invades non-competitive plant communities quite quickly, was less influenced by soil disturbance and historical land-use intensity. Tall dropseed was also the most frequently recorded native grass; it was particularly evenly distributed among land-use types and had often invaded roadsides dominated by Kentucky bluegrass.

Indian grass, switchgrass, and Canada wildrye were most influenced by land-use history and were frequently associated with woodlands, suggesting that wooded areas may serve as native-grass refugia, harboring propagules that colonize roadsides after road construction. Other studies have found a similar relationship between prairie remnants and woodland. In Illinois, prairie remnants were found to be concentrated along the forested valleys of the Illinois and Mississippi rivers (White 1981). Evidence exists to suggest that many prairie or savanna remnants have succeeded to woodland in the wake of fire suppression. Many areas in Ohio, known historically as prairie, now support woodlands (Transeau 1981). In Missouri, McCarty and Hassien (1986) documented the positive growth response of native-grass clumps after a forest clear cut. They suggested that prairie plants beneath a woodland canopy are probably residuals from a historically more predominant prairie understory, and noted that succession to forest had not extirpated the prairie flora.

This study suggests that woodlands may contain more, viable prairie remnants than commonly realized and supports the hypothesis advanced by Hamilton (1992) that many Iowa woodlands may have originally been savannas. In Lee County, wooded areas appear to contribute more to the natural reestablishment of prairie roadsides than do areas originally dominated by prairie and currently in cropland. Prairie plants were probably more predominant in woodland understories prior to fire suppression. Low land-use intensity in woodlands has apparently sustained the prairie understory component long enough for it to recolonize seldom-disturbed roadsides.

Individuals or programs seeking to identify roadside prairie remnants for seed collection or management might find it efficient

Table 4. Comparison of expected and observed roadside native grass species distribution among adjacent land-use types in Lee County, as based on confidence intervals.

		Observed proportion[a]				
Land use	*Proportion expected*	*Big bluestem*	*Canada wildrye*	*Indian-grass*	*Switch-grass*	*Tall dropseed*
Cropland	54.9	51.2	54.3	49.9-[b]	49.1-	55.7
Hayfield	10.9	11.0	10.9	8.2	10.5	10.4
Pasture	20.2	21.	17.7-	22.1	20.9	20.7
Woodland	14.2	16.1	17.1+[b]	19.7+	19.5+	13.2
Total	100.0	100.0	99.9	100.0	100.0	

[a] Observed proportion i = $\frac{\text{frequency of species i in samples with land use j}}{\text{total frequency of native grasses in samples with land use}}$

[b] Significantly less (-) or greater (+) than expected ($P < .05$), based on confidence intervals for proportions (Neu et al. 1974, Byers et al. 1984).

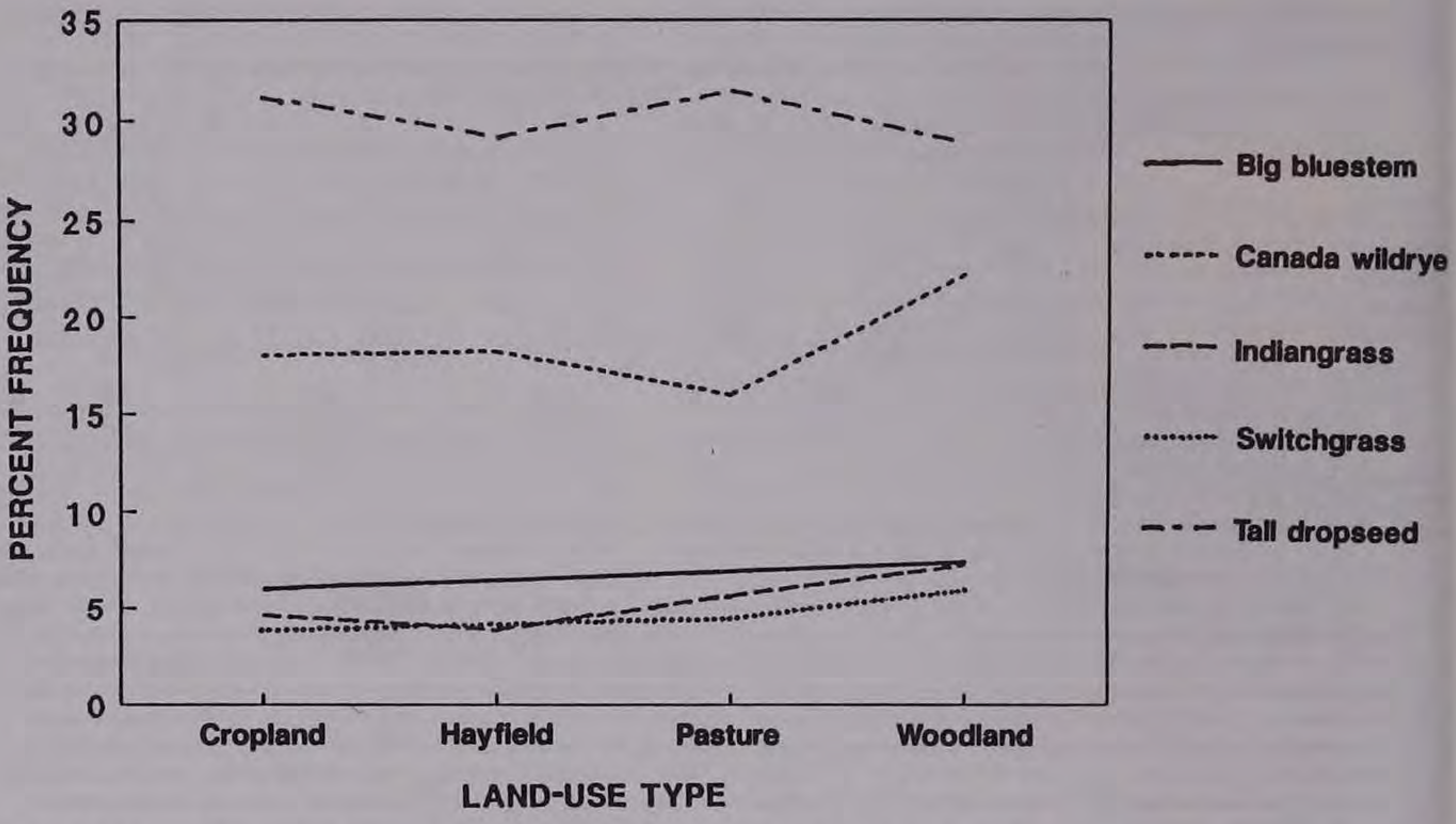

Figure 2. Percent frequency of native grasses in Lee County roadsides, in relation to adjacent land-use type

to concentrate their efforts in or near areas with less intensive land-use histories, as indicated by woodlots and small tracts of forest. The occurrence of prairie species within woodlands suggests that, by cutting and burning, prairie or savannah could be restored. In central Missouri, the Forest Service is attempting such restoration (McCarty and Hassien 1986).

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PRAIRIE RESTORATION: A TWENTY-FIVE YEAR PERSPECTIVE ON ESTABLISHMENT AND MANAGEMENT

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Abstract. Conclusions drawn from twenty-five years of prairie restoration experience are reviewed. Fire management of various prairie habitats, need for more frequent burning, benefits of early spring burns, and effects of fire are discussed. Grass-forb competition, cold-damp seed conditioning, watering, and seed quality are also considered. Differential conditioning of grass and forbs is described and advocated. Mosaic planting procedure is described and evaluated. Weed control by germination and scratch-out of the top-most portion of the weed seed bank and its relationship to time of planting is reviewed. A scheme of developmental stages for prairie restoration is proposed with dominant species, descriptive attributes, competitive processes, and approximate duration of the various stages described and discussed. Forbs are grouped in overlapping assemblages of occurrence in this successional stage framework, with staying-power and quality indicated. Concern is voiced about the monocultural switch grass syndrome and the use of inappropriate prairie grass ecotypes in wildlife habitat plantings and roadside prairies. The importance of burning and proper seed mixes for roadside restorations is discussed with specific mixes suggested.

INTRODUCTION

Natural areas restoration is a realm of ecology destined to become the single most important environmental effort of the future. With the demise of tropical rain forests, the clear-cutting of ancient old growth forests of the Pacific northwest, and the continued cutting of oak-hickory stands in the Midwest for firewood and industrial pallets, to name a few examples, it is becoming increasingly clear that preservation efforts cannot begin to keep up with the destruction. Unfortunately, some of these habitats, once destroyed, cannot be restored in a single lifetime or even several lifetimes. Restoration ecology for many of these habitats is in its infancy.

This is not true for prairie restoration. We know quite a bit about this process. Unfortunately, with all the current interest in and efforts at restoration, what we know is not being used. Current literature is too vague and noncommittal about how to restore a prairie. On the one hand there are papers by scientists, whose cautious, experimental, and scholarly approach is little help in guiding the practical process of establishing a prairie planting. Then there are brochures by commercial companies selling prairies. Some are well done and quite informative; others are misleading or actually damaging. Additionally, some publications by public agencies are so general and noncommittal that they do not guide the new restorationist to a practical and realistic process that will result in the best prairie planting possible under the given circumstances.

Because of this, I decided to review and discuss what I have learned in more than 25 years of prairie restoration. It has been mainly a process of trial and error. The initial work was done on the Knox College Biological Field Station, located 20 miles east of Galesburg, Knox County, in west-central Illinois. After many years of experimental planting at the field station, I began commercial plantings at state parks and wildlife areas, federal refuges, public and private school grounds, and private projects of all kinds, including Conservation Reserve Program (CRP) plantings for farmers in Illinois, Iowa, and Indiana. I currently do about 25 prairie plantings a year. I am still learning and adjusting my restoration process as I begin new plantings, evaluate already established projects, and watch the oldest plantings on the Knox Field Station and elsewhere.

I do not "know it all" when it come to prairie restoration, but I have found it necessary to be somewhat dogmatic and outspoken to get key points across. New restorationists do not seem to learn from the mistakes of others. I guess it's human nature, but they love to go off on their own and make their own mistakes. But prairie restoration takes long enough to do using correct procedures; why extend the process by repeating past errors. My main goal has always been to find the most practical way to restore a true prairie. The process is not all that difficult if done properly. Some points emphasized here have been made in past publications (Schramm 1978) but need re-emphasizing. Others, such as the proposed successional stages of prairie restoration, are new and undoubtedly will be revised or added to in the future.

This paper applies primarily to the high rainfall regions of the tallgrass prairie. Some points may apply to restoration in the dryer Great Plains region, but I have had no restoration experience in those regions.

The models for restoration are the prairie remnants. I have looked at prairie remnants all over the Midwest. I have talked at length and gone into the field with some of the most knowledgeable prairie botanists to try to understand what constitutes a good, true prairie. This is elusive information. My most important mentors in this process have been Dr. Robert Betz of Northeastern Illinois University and Ray Schulenburg, formerly of the Morton Arboretum, both of whom gave me important insights into what constitutes true, quality prairie. Dr. Robert Livingston, formerly of the University of Massachusetts, introduced me to and helped me key out my first prairie grasses, and Aldo Leopold introduced me to my first prairie wildflowers when I was a young boy. So, to the new restorationist I say, much has gone on before, and I urge you to profit by the experience of others.

FIRE MANAGEMENT

One would think that by now, fire would be universally accepted and vigorously applied in all restoration and management efforts, but fire is still being used too conservatively. Many prairie preserves are not burned often enough or thoroughly enough or at the right time. Hill prairies and glade prairies are being lost to eastern redcedar (*Juniperus virginiana*) and other woody plant invasion through lack of coordinated, dedicated efforts to burn them at the right time.

These recommendations apply mostly to the high rainfall regions of the tallgrass prairie, where, in normal years, post-burn productivity is enhanced by adequate spring and summer rainfall.

When To Burn And The Effects of Fire

There is only one time to burn — early spring. There are usually several days to a week or more of ideal burning weather during March and one must be poised and ready. If you miss it, you can run into trouble getting the burn done later. Occasionally, these ideal conditions occur in February, but you need some sunny conditions, warming, and a moderate breeze to burn efficiently. We like to have all burning completed by mid-April.

Early spring burning leaves winter cover for wildlife. More important, it clears away accumulated litter and produces black ash, which in combination with sunlight warms the soil and stimulates early prairie plant growth at a time of maximum moisture. In effect, this lengthens the growing season for warm-season prairie plants. Litter removal appears to be the primary factor in beneficial response of prairie to burning (Anderson 1982; Knapp and Seastedt 1986).

A common misconception is that the primary advantage of burning is killing or suppressing non-prairie species, thereby releasing the prairie species from competition. There is some suppression, but the main effect of a properly timed fire, is to stimulate the prairie species which then outcompete the non-prairie species. This misconception about fire suppression of non-prairie species has led people to burn later in the spring or in early summer, believing they are killing cool-season, non-native forbs and grasses when, in reality, they are stressing the warm-season natives that are just entering peak growth. Fall burns, after the prairie has gone dormant, do not suppress the prairie but do lack the advantage of the sudden ground-warming effect that a spring burn produces because ash from a fall burn is washed away by winter precipitation.

That ash provides a nutrient boost is an older idea that has been very hard to demonstrate (Old 1969). The role of fire in mineral cycling and increasing or decreasing available nitrogen(N) is still not clear. Old (1969) reports higher N levels in plants from burned areas while Seastedt and Remundo (1990) conclude that frequent burning creates conditions for severe N limitation to plant productivity. Recent reviews (Collins and Wallace 1990) emphasize that there is still much to learn about the effects of burning, but one thing is obvious—prairies in high rainfall areas, restorations and remnants included, greatly improve with regular burning.

Frequency of Burning

Remnants.

How frequently the original prairies burned does not have much bearing on determining frequencies for management. Most remnants have been neglected or abused by grazing, haying, and other disturbances and currently need regular burning to regain their original quality. For a typical remnant, half the area should be burned each year, providing unburned, survival refugia for possible endemic insect life history stages. Lack of knowledge about prairie insects calls for this conservative approach. After a decade, if recovery and improvements are evident, an every three-to-four year burn for each half of the remnant can be scheduled. Other studies have concluded that a three-year burning interval was necessary to maintain grass dominance and the species diversity typical of native prairie (Kucera and Koelling 1964; Kucera 1970).

Restorations.

Restorations are a different matter entirely. Prairie restoration is, plainly and simply, a process of manipulating perennial, herbaceous plant succession. All restorations, during the first decade or so, need burning every year to speed up establishment and seral progression of prairie plant succession. There is no need to worry about the survival of endemic insects because, in most instances, they are not present yet (Selser and Schramm 1992). The idea, circulated some years ago, that one should not burn the first spring after planting, is incorrect. Restorations develop and improve more quickly if burned every year for at least five years, including the spring after the first year's growth. The one exception is on steep slopes where severe erosion may have exposed the new root systems and fire could damage the vulnerable meristem of these hemicryptophytes.

The first year or two, it is sometimes difficult to get a good burn. Annual weeds, such as foxtail (*Setartia* sp.), and old witch grass (*Panicum capillare*), are usually present and may aid in providing fuel for these all-important first burns. With regard to long-term, continuous burning, the best prairie plots on the Knox College field station are those that have been burned every year for over two decades. As with the remnants, after a restoration is well-established and progressing nicely, alternate year burns on one half of the area would be prudent with the hope of encouraging insect endemics. In any event, after the first two decades, portions of a restoration should be burned at least once every three to four years to encourage progression to a climax equilibrium.

Burning of Special Kinds of Prairies

Hill and glade prairies.

The loess and limestone hill prairies of the Midwest and the glade prairies of the Ozarks are in serious trouble from lack of burning. The problem is that most of these sites have been severely overgrazed, allowing invasion of prickly woody plants, such as eastern redcedar, that are avoided by livestock. Eastern redcedar is the single, most serious threat to these xeric prairie remnants, but burning can solve the problem. Fortunately, eastern redcedar is very fire-sensitive. Seedlings are usually killed outright by one or more burns. Even larger trees can crown-out from a ground fire and be killed. Burning hill prairies and glades is not easy, but it is essential.

Sand prairies.

We are just learning about the effects of burning sand prairies. My personal observations Big River State Forest in Henderson County in west-central Illinois indicate a rapid improvement in the vigor of the prairie species—dominant grasses little bluestem (*Andropogon scoparius*) and June grass (*Koeleria cristata*) and a number of sand prairie forbs. The rare sand forb, giant penstemon, (*Penstemon grandiflorus*) is thriving and increasing with the new fire management program. Furthermore, there was a definite suppression of the prickly-pear cactus (*Opuntia rafinesquii*), a grazing-disturbance, successional species that dislikes fire. Where cactus is well established, it will take several burns to really knock it out.

Savannas.

There is current great interest in savanna ecology, preservation, and management (see this proceedings). It is fire that created savannas the world over. All the true prairie plants and savanna-specific species appear to thrive under a rigorous burning regime. A word of caution—in savannas that have not been burned for some time, great care should be exercised to prevent the fire from burning up into the inner hollows of old burr oaks, white oaks, and hickories. In old trees, which may not have been subjected to fire for many years, such inner-core burning can weaken and topple them, thus, losing a key feature that makes a savanna.

Mowing and Grazing versus Burning

Some think mowing or grazing can substitute for burning. This is wishful thinking. Mowing and grazing are special kinds of disturbance that result in incomplete litter removal and, depending on when they occur, may suppress photosynthetic productivity. Betz (1989) found annual mowing of hay prairies completely suppressed the reproduction of Mead's milkweed (*Asclepias meadii*). Grazing by large ungulates was a naturally occurring process in climax, temperate grasslands that, because of migratory and nomadic movements, probably had only transient and localized effects on the vegetation. Grazing by native ungulates is now being studied at the Konsa Prairie in Kansas, and important new insight into this process should be forthcoming.

If you think you are in a situation where you cannot burn, do something to reverse the situation or don't get involved in prairie. If you try prairie without fire, you'll have poor results and a negative impact on the prairie movement.

GRASS-FORB COMPETITION

Perhaps the most important insight gained in over two decades of prairie restoration is in regard to grass-forb competition. In the early years, we worried about the non-prairie weeds out-competing the prairie (see Control of Non-native Weed Competition below).

but we soon learned that, by the vigorous and regular use of fire, the prairie would eventually win over the weeds. The more serious problem was the prairie competing with the prairie. Ultimately, competition between grasses and forbs determined the nature of the stand, and this, in turn, was determined by what went into the ground the initial day of the planting. To phrase this another way, "What you plant is what you get!". So we began to work on solutions for this grass-forb competition and came up with mosaic planting and differential seed conditioning.

MOSAIC PLANTING

The Case For

Mosaic planting is the simplest and most reliable way to prevent tall grasses from overpowering forbs in later stages of prairie plant succession. It involves inserting one or more forb plantings into a general prairie planting. This procedure has been so successful, I almost always use it. Also, I feel this more closely approaches the original prairie. Tallgrass prairie was not a uniform stand. To the contrary, the remnants that are our models are all different. Some are grass dominated; others are forb dominated; still others consist of mixed patches of forbs and grasses, in various combinations throughout the remnant. A restoration should try to duplicate this mosaic. With few exceptions and regardless of the intended use of the stand, a diverse mosaic provides the best habitat. One of the underlying principles of modern Ecology is that diversity is associated with the stability of many healthy, natural ecosystems. Wildlife managers have long recognized that wildlife of all kinds are drawn to and thrive in a diverse mosaic of habitat types. This diversity is part of the esthetic beauty of a quality prairie. Mosaic planting is a step in the direction of trying to duplicate what we observe in nature.

The Procedure

In mosaic planting, one or more areas of the planting are loaded with a forb mix while reducing tall grasses to only a pound per acre rate or less. Because they develop slowly and present no competitive threat to the forbs, little bluestem and prairie dropseed (*Sporobolus heterolepis*) can be used quite liberally in such mixes. These forb-dense sections can be placed in sites that I call viewing areas — in the foreground, near a trail, or next to a road. In background areas, the taller grasses can be increased to four to eight pounds, still including many forbs in the mix. In another area, a dense planting of ten to fourteen pounds of tall grasses per acre can be applied with some of the more competitive forbs still included. The final result, if done properly, is a diverse prairie landscape that is pleasing to the eye and is suited to a wide variety of uses. This approach can be used on areas of all sizes. I use a specially modified Nisbet rangeland grass drill on all sites, even those less than one acre, and by drilling round and round over the selected portions of the site, I can achieve the desired mosaic placement of the various mixes.

The process is not an exact science; no two mosaic plantings are alike. Wilson (1970) pointed out that planting with a Nisbet drill is an art. Mosaic planting is, likewise, somewhat of an art form, with the drill being the brush, the seed mixes the paint, and the operator the artist. With some experience, the operator can arrive at a site and quickly determine where the best viewing areas for forbs will be and where the denser grass stands should be placed. The result, though variable from site to site, is an acceptable facsimile of what we believe the original prairie was like.

SEED CONDITIONING

Cold-damp conditioning, or stratification, has long been recognized as necessary for breaking dormancy of dry seed and assuring prompt germination (Schramm 1978), which is critical for quick establishment. All prairie forbs, except legumes, can profit from cold-damp treatment. The smaller the seed, the shorter the time required. Tiny seeds of spring-blooming species, such as shooting stars (*Dodecatheon meadia*), alum root (*Heuchera richardsonii*), and pale-spiked lobelia (*Lobelia spicata*), need only one to two weeks. A few of the softer, larger seeds such as the milkweeds (butterfly weed *Asclepias tuberosa* and the various green milkweed species), likewise require only two to three weeks of cold-damp to germinated freely. But most of the prairie forbs successfully used in current restoration, such as the silphiums, coneflowers, blazing stars, and rattlesnake master, need six to eight weeks of cold-damp to germinate promptly. A few toughies with hard seed coats or perhaps more complex conditioning chemistry need longer periods to break dormancy. I have found that the hard, grey, rock-like seeds of spiderwort (*Tradescantia ohiensis*) need four to six months of cold-damp. New Jersey Tea (*Ceanothus americanus*) was found to give maximum germination (70%) only after boiling water treatment of one to two minutes followed by six months cold-damp conditioning (Schramm and Johnson 1981). Legumes germinate readily without cold-damp treatment if they are lightly scarified by scratching in a sandpaper box, moistened, and inoculated with the appropriate *Rhizobium* bacterium.

Moisture and Temperature

Some restorationists treat their seed with cold only, but for really quick germination, the seeds must be moistened, but only slightly! It takes very little dampening to achieve complete conditioning. Do not get the seed wet. This makes it difficult to handle later. One part water, by volume, to fifty parts seed is adequate. Do not add other substances such as sand or vermiculite. They are unnecessary and will foul up your planting devices. For small amounts of the tiniest seeds, a little potting soil may be added, but most prairie seed has enough chaff to hold the moisture needed for conditioning. The ideal temperature for conditioning is just above freezing, one to two degrees C.

DIFFERENTIAL CONDITIONING

In recent years, I have used a differential seed conditioning to help counteract the problem of prairie grasses out-competing forbs. In addition to reducing rates of grass seeding, I leave the grass somewhat more dormant than the forbs. This is accomplished by cold-damp conditioning the forbs (legumes excepted) while leaving the grasses dry. Then, when these two groups are mixed together and planted, given adequate moisture in the soil, the forbs will germinated almost immediately while the grasses will delay from one to three weeks. In mixed plantings, this gives the forbs an advantage over the grasses at this initial stage of establishment. The grass seed is open-air dried on the floor of an enclosed building for four to five weeks, then bagged in plastic bags to retain some moisture, and stored in cool or cold (either works well) conditions. The resultant seed will store well without molding, has some degree of dormancy, but will germinate more rapidly than grass seed that has been dried completely and stored in the open mesh bags used by most commercial producers.

MOISTURE FOR GERMINATION

Recent experience has shown that extra precipitation or watering can greatly enhance initial germination and seedling establishment. Experiments with extra watering, even in normal rainfall years, on newly planted prairie gardens and other small plots with available irrigation have resulted in quick establishment and increased growth. No matter how wet the year, if you can water thoroughly right after planting, by all means, do so. After that initial heavy soaking, water once a week for several weeks for really good establishment, especially of the forbs.

QUALITY OF SEED

It is imperative to use the best seed you can find. A few seeds sown in flats, watered, and germinated after proper conditioning can tell you much about the future success of your planting. Jim Wilson (1970) discussed this at the first prairie conference. He pointed out that even though it germinates, live seed from a batch with low percentage germination is weak seed, and we have found this to be very much the case. Whether you harvest your own grass or buy from a supplier, take an individual seed, pinch it gently at the base with the nails of the thumb and forefinger, and squeeze the kernel out of the glume and lemma. If it is fat and filled out, you've probably got a good product that will result in good stand establishment. The same holds true for forb seed. Get a magnifying glass or dissecting scope and spend some time studying your seed. It is worth the effort.

CONTROL OF NON-NATIVE WEED COMPETITION

Non-native weed competition remains the most unpredictable variable in restoration planting. Much has been written about this (Schramm 1970 and 1978, Wilson 1970). Earlier in this paper, I made the statement that "What you plant is what you get," but the final product is also influenced by the amount of annual weed competition at the very beginning of the restoration. Some prairie species can compete at this early succession stage, and others cannot. So control weeds as much as possible before the actual planting. Many projects are not as good as they might be because of poor planning and timing of site preparation—working the ground and getting those annual weed seeds of the shallow, surface seed bank germinated and scratched out.

Site Preparation Is The Key

Perennial root situations.

If there is perennial vegetation present (pasture sod, hay fields, lawns, etc.), the site should be plowed or tilled in the fall so that frost can kill any perennial grass or forb roots during the winter. If the site is fallow from previous farming and has only annual weeds present, ground preparation can wait until the following spring.

Spring site preparation without chemicals.

Before planting, disc and harrow the site as early as the ground can be worked. Harrowing (or other final leveling) is essential for smooth, even ground. Then, in future years, one can walk in the plot without stumbling on rough ground. After the ground is harrowed smooth, wait two or more weeks until some weeds have come up. Then use a harrow, harrowgator, cultimulcher, or similar implement to scratch out the germinating weeds. Do this two or more times during April, May, and into June, if necessary, so several generations of weed seeds can germinate. Of course, it is impossible to eliminate all weeds, but this repeated shallow working will reduce much of the potential weed competition. The key point is to work just the surface of the soil. If the site is deeply worked by rototilling or deep discing, the procedure is defeated by bringing up more weed seeds from the deeper part of the seed bank. You are at the mercy of not only the equipment operator but also the weather.

Spring site preparation using Round-up.

Another alternative is chemical treatment. Two or more weeks after the site is disced and harrowed to a smooth surface, the emerging weed seedlings are treated with Round-up, a non-residual, short-term, broad-spectrum herbicide. This herbicide, available from elevators and farm supplies stores, is sprayed on actively growing weeds at the 2 to 5 inch stage, using a 1.0% to 1.5% solution on annuals and a 2.0% solution for perennials. Two or, ideally, three treatments are desirable, depending on the weed problem. After Round-up treatment, do not rework the ground; this will only bring up more weed seeds. Six or more days after the last Round-up treatment, the prairie can be planted into the firm, weed-free seed bed. A good prairie seed drill can cut the seed in without any more tilling. In some projects excellent results have been obtained by combining one or more mechanical scratch-outs with a final Round-up treatment.

All site preparation calls for planning, proper timing, proper equipment, and, most of all, the operator's commitment to follow the plan. One can still get prairie establishment without doing the site preparation perfectly, but many prairie projects could be greatly improved by commitment to this part of the process.

The problem of fall plantings.

By now, it is obvious that late spring or early summer is the best planting time because it allows one to get control of annual weeds. Conversely, a fall planting presents numerous problems in this regard. First, prairie seed will be dormant over winter, during which time animals will consume some of that precious and expensive seed. In addition, the cool-season weeds have not only the fall, but the long, cool spring to germinate. Warm-season prairie seeds need damp, hot soil to germinate, and by the time such conditions occur in late May, the annual weeds have a big advantage. Prairie restoration is a plant successional race with many participants competing for the lead. Don't let the annual weeds get that lead.

DEVELOPMENTAL STAGES OF RESTORATION SUCCESSION

A thorough understanding of plant succession is important to successful prairie restoration. With the earlier restorations now in

Table 1. A proposed scheme for developmental stages in prairie restoration.

Stage #	*Plant name*	*Descriptive name*	*Years*
I	***Rudbeckia* stage** (blackeyed susans)	**Initial downgrow, weedy stage**	**1-3**
II	***Ratibida-Heliopsis* stage** (yellow cone flower, false sunflower, rosenweed)	**Intense competitive, stand establishment stage**	**2-5**
III	***Eryngium-Silphium* stage** (rattlesnake master, compass plant, prairie clover, prairie dock)	**Closeout stage**	**6-12**
IV	***Amorpha-Sporobolus* stage** (lead plant, dropseed, culver's root)	**Longterm Adjustment stage**	**13-20+**

Table 2. Developmental stage amplitude of prairie plant species

SP=Staying Power SP+=Staying Power Plus CS=Competition Sensitive A=Aggressive

	StageI	StageII	StageIII	StageIV
Composites				
Blk-Eyed Susan (*Rudbeckia hirta*)	------------>			
Yellow Cone Flower (*Ratibida pinnata*)		--------------->		
False Sunflower (*Heliopsis helianthoides*)	------------------>			
RosinWeed (*Silphium integrifolium*)		------------------>		
Compass Plant (*Silphium laciniatum*)			------------------>SP+	
Prairie Dock (*Silphium terebinthinaceum*)		------------------------>SP		
Cup Plant (*Silphium perfoliatum*)		-------------Wet Mesic----------->		
Stiff Goldenrod (*Solidago rigida*)		------------------------>SP		
Showy Goldenrod (*Solidago speciosa*)		------------------------>		
Old Field Goldenrod (*Solidago nemoralis*)		-------------------------->SP+		
Rough White Lettuce (*Prenanthes aspera*)			----Dry Mesic------>	
Smooth White Lettuce (*Prenanthes racemosa*)			----Wet Mesic------>	
New England Aster (*Aster novae-angliae*)	----------Wet Mesic-------->			
Prairie Blazing Star (*Liatris pycnostacya*)		-------------------------->CS		
Rough Blazing Star (*Liatris aspera*)		------------------------>		
Pale Purple Cone Flower (*Echinacea pallida*)		------------------------------>		
Purple Cone Flower (*Echinacea purpurea*)	------------Savanna------->			
Wild Quinine (*Parthenium integrifolium*)			--------------------->	
Prairie Coreopsis (*Coreopsis palmata*)			------------------->	
Heath Aster (*Aster ericoides*)		----------------------->		
Sky-blue Aster (*Aster azureus*)			--------------------->	
Smooth Aster (*Aster laevis*)			--------------------->	
Grasses				
Switch Grass (*Panicum virgatum*)	-------------------------------------->A+			
Big Bluestem (*Andropogon gerardii*)		------------------------------>A		
Indian Grass (*Sorghastrum nutans*)		--------------------------------->SP		
Little Bluestem (*Andropogon scoparius*)			------------->SP	
Prairie Dropseed (*Sporobolus heterolepis*)			------------->SP	
Legumes				
Showy Tick Trefoil(*Desmodium canadense*)		------------------------------------>SP		
Illinois Tick Trefoil (*Desmodium illinoense*)		------------------------->SP		
Round-headed Bush Clover (*Lespedeza capitata*)		--------Dry to Wet Mesic----->SP		
Purple Prairie Clover (*Petalostemum purpureum*)			----Dry Mesic----->SP	
White Prairie Clover (*Petalostemum candidum*)		----------Mesic------->SP		
White False Indigo (*Baptisia leucantha*)		----------------------->SP		
Cream False Indigo (*Baptisia leucophaea*)			----------->CS	
Lead Plant (*Amorpha canescens*)			----------->CS	
Umbels				
Rattlesnake Master (*Eryngium yuccifolium*)		--------------------->SP+		
Golden Alexanders (*Zizia aurea*)		-------Wet Mesic------>		
Mints				
Mountain Mint (*Pycnanthemum virginianum*)		------------------------>		
Wild Bergamot (*Monarda fistulosa*)		---------------------------->		
Others				
Culvers Root (*Veronicastrum virginicum*)			------------------>SP+	
New Jersey Tea (*Ceanothus americanus*)			-------------------->	
Prairie Cinquefoil (*Potentilla arguta*)			-------------------->	
Spiderwort (*Tradescantia ohiensis*)			-------------------->SP+	
Yellow Gentian (*Gentiana flavida*)			------------------->SP	
Bottle Gentian (*Gentiana andrewsii*)		---------Wet Mesic------->		
Prairie Gentian (*Gentiana puberula*)			--------->	
Penstemon (*Penstemon digitalis*)		-------------------------->		
Butterfly Weed (*Asclepias tuberosa*)			------------------->CS	

Nomenclature after Jones, 1971

their third and in some cases forth decade, we are in a better position to understand and describe successional stages of this process. Based on two decades of observations at the Knox College field station and various other restorations in Illinois and Iowa, I propose the following successional stages in prairie establishment. It is not in final form or complete by any means, but is offered as an initial format to be developed and added to as additional years of observations increase our insights into prairie community developmental processes.

I have divided the succession process into stages that are identified by a stage number, a plant-(or plants) stage name, and a descriptive name (Table 1). An approximate number of years covered by the stage is also proposed. This time element is the most variable part of the proposal and differs depending on weed competition and the nature of the restoration. A more detailed scheme (Table 2) presents most of the prairie species I have worked with, showing where they fit into this successional progression. The dotted, amplitude arrows indicate where in the progression, each species becomes an obvious part of the community. The term staying-power, introduced here, is a useful characteristic denoting the ability of a species to persist and even to increase as the community develops and matures. The ability of a prairie species to persist and eventually spread depends on whether that species is in the optimum part of its ecological amplitude as expressed both by habitat and associated species. It also depends on the seed dispersal mechanism of the species. Our understanding of these associations and characteristics, is still in its infancy.

Discussion Of The Stages

Stage I.

Stage I, the *Rudbeckia* Stage, or the **Initial Downgrow Weedy Stage**, lasts two to three years after planting and is characterized by the dominance of prairie annuals, such as black-eyed susans (*Rudbeckia hirta*); the non-native annual weeds, such as foxtail grass (*Setaria sp.*), old witch grass(*Panicum capillare*), velvet leaf (*Abutilon theophrasti*), lamb's quarter (*Chenopodium album*), pigweed (*Amaranthus sp.*), and the native ragweed species (*Ambrosia sp.*). Because new prairie plantings look so messy and un-prairie like, this stage gives a bad impression to the uninitiated. This is the time when the prairie species are "growing down" rather than up (Wilson 1970). Three to four weeks after germinating, a prairie grass species such as big bluestem (*Andropogon gerardii*) and a prairie forb such as compass plant (*Silphium laciniatum*) may be only one to two inches tall, but the roots will have grown more than a foot into the soil. At the end of the first growing season, prairie species may still have only six inch, wispy tops buried in the foxtail and difficult to even find, but the roots will be well established, two or more feet deep. This is when the new restorationist must apply those two necessary ingredients, patience and fire, if the project is to succeed. Just how much the annual weeds dominate this first stage is extremely variable and unpredictable (Schramm 1978). It depends on how much weed seed was in the surface seed bank and how successful weed control procedures were (see Weed Control above).

Stage II.

Stage II, the *Ratibida-Heliopsis* Stage, is named after yellow cone flower (*Ratibida pinnata*) and oxeye, or false sunflower (*Heliopsis helianthoides*), two prairie species typical of this second stage of development. Other species prominent during this stage are rosenweed (*Silphium integrifolium*) and others listed in Table 2. This is also the **Intense Competitive, Stand Establishment Stage,** referring to the intense, competitive processes that are going on among the prairie species themselves as they vie for space and resources during this phase of community development. This is the first really colorful stage, with the dominant, yellow-flowered species making an impressive and pleasing display. This stage begins in the second or third year and may last three to four years or longer as the prairie matrix (Betz 1986) becomes evident (see discussion below). The larger grasses also become prominent, and it is apparent if too much grass has been used or if the grass seeding rate has been properly balanced against the forb seeding rate. Species with staying-power are not yet dominant but show here and there; the competitive processes that will determine the final nature of the stand are well under way. Most annual weeds are gone. Velvet leaf disappears the second year. Annual fleabane (*Erigeron annus*) disappears the fourth or fifth year. More persistent, perennial, non-prairie weeds, such as tall goldenrod (*Solidago altissima*), are still present and seem to be holding their own. Annuals, such as little ragweed (*Ambrosia artemisiifolia*), are, by now, reduced to miniature stature — still growing but like bonsai plants tucked into the prairie matrix. The colorful prairie annual, black-eyed susan is still re-seeding itself but has moved to the edge of the stand.

Stage III.

Stage III, the *Eryngium-Silphium* stage, is named after rattlesnake master (*Eryngium yuccifolium*), compass plant (*Silphium laciniatum*), and prairie dock (*Silphium terebinthinacium*), which now begin to flower for the first time. Purple and white prairie clovers (*Petalostemum purpureum* and *P. candidum*) are also evident and flower regularly. In this **Closeout Stage**, most of the annual weeds have been eliminated (the ragweeds are gone and the perennial tall goldenrod clones are being suppressed) and the dominant prairie forbs of Stage II are being pushed to the edge of the stand. This movement-to-the-edge phenomenon is not entirely new—in Stage II we saw the movement of black-eyed susans to the edge as the perennial species increased their toehold. Stage III persists six to twelve years or longer, during which time the stand may be evaluated with regard to what species have been successfully established and what can be expected in the future. At this point, the staying-power forbs, such as spiderwort (*Tradescantia ohiensis*), Culver's Root (*Veronicastrum virginicum*), rattlesnake master, the climax silphiums (compass plant and prairie dock), prairie cinquefoil (*Potentilla arguta*), sky-blue aster (*Aster azureus*), and others, are really coming into their own.

Stage IV.

Stage IV is the final stage described in this proposal but is probably not the final stage of this process. This is the **Long-term Adjustment Stage,** or the *Amorpha-Sporobolus* Stage, named after lead plant (*Amorpha canescens*) and prairie dropseed (*Sporobolus heterolepis*), which finally begin to flower and make a real showing, if present. This stage, in older restorations, reveals much regarding staying-power of various species. In the center of the stand, closeout of the more successional prairie species has been completed and long-term adjustment has begun among the remaining, more mature, climax community species. The time frame proposed is thirteen to twenty or more years. Thirty, forty, or more years are possible. The limits, if any, on this stage will be determined by future observations.

Discussion

Betz (1986) has presented valuable insight into and a detailed description of plant succession during the first decade of a prairie planting at the Fermilab in Batavia, Illinois. In this discussion, he introduced the concept of the prairie matrix, an assemblage of more aggressive, competition-tolerant prairie species that, with regular burning, establish early and constitute the primary competitive force that suppresses and eventually eliminates the non-prairie weed species. In my scheme, Betz's matrix is well-established by the end of Stage II and has closed out the non-prairie weeds by the end of Stage III. Betz suggested that later, more competition-sensitive prairie species may be added to this matrix assemblage. I agree, although in some of our restorations, competition-sensitive species survived being planted at the outset and eventually came into their own in Stage IV.

One of the curious occurrences observed in many restorations is that each year, even into the second decade (or well into Stage III), new species appear. These species were in the original seed mix but did not appear until years after the initial planting. Betz (1986) observed this, and we have seen it a number of times. We do not know whether the seeds lay dormant for a number of years or germinate but remain inconspicuous, buried in the vigorous growth of the more aggressive, successional species. I suspect the latter is, generally, the case. Our work with conditioning and germination suggests that even the hardest seeds, such as the legumes and spiderwort would germinate by the third year.

Sperry (1983) gave additional insight into the late stages of prairie restoration in his analysis of the oldest restored prairie in the eastern tallgrass region, started in the 1930s at the University of Wisconsin Arboretum in Madison (the Knox College project is the second oldest restoration, started in 1955). Many of the forbs that Sperry reported persisting in the Wisconsin restoration also persisted in the Knox College prairie and other restorations I have planted. These are the species I designated as having staying-power. Sperry reported that some quality species did not spread, or actually decreased, in the Wisconsin restoration. I do not know the exact burning history of that project, but I do know there have been several interims of infrequent fire that, I suspect, limited establishment and spread of some species.

My attempt to formalize successional stages in prairie restoration obviously has its limits of usefulness. Experienced restorationists may take issue with my choice of species used to characterize the stages. No two restorations are exactly alike. The time frame may be greatly protracted in some establishments because of local adverse conditions, or it may be greatly accelerated because of reduced weed competition, ideal moisture, particularly good seed, or a host of other reasons. Prairie restoration is still more of an art than a science and is at the mercy of many variables that we are still learning to control. But stages do exist, and this proposed scheme may facilitate talking about the processes and comparing observations. I hope this will help new restorationists understand and evaluate what is happening in their projects.

Mix Composition Decisions

It is hoped that the Successional Stages and associated plant lists will be useful in determining mix compositions for new restorations, but if seed is available and costs are not prohibitive, there is nothing wrong with including Stage III and IV species in the initial planting. Sometimes they do quite well for reasons we cannot explain. For most quality forbs, the more seed planted, the better the results. We still strongly advise against planting the really weedy species of sunflowers (*Helianthus mollis*. *H. grosseserratus*, etc.) because of their vegetative spreading and allelopathic properties (Schramm 1978).

THE ECOTYPE PROBLEM

At the first prairie conference, held at Knox College in 1968, no concern was voiced about the source of seeds for local restorations. We were all so caught up with the urge to restore, planting methods, limited seed availability, etc., that no one was really thinking about the genetics or purity of restoration. But two years later, at the Wisconsin prairie conference, Jerry Schwartzmeier voiced great concern over preservation of local gene pools. We can all thank erry for calling this to our attention; it was a timely warning that most of us took to heart. Biologists and other knowledgeable people from many of the disciplines and agencies interested in using prairie plantings responded immediately and in a positive way to this concern. It was well known that naturally selected ecotypes, or genetic variants adapted to local conditions, existed within species of prairie grasses and forbs. It made common sense to most of us to use local seed sources. First, if the prairie planting is to be a restoration, then we should try to restore what was there originally. Second, we should be concerned with the preservation of local gene pools as part of the vast genetic diversity of this once wide-spread plant community. And finally, natural selection has already determined that these local genotypes are the ones that are best suited to local conditions.

Thus, the purist approach was initiated. Judging from my contacts with hundreds of restorationists over the last two decades, more than 90% take this approach. To the vast majority, whether or not to use local strains is not even a debatable issue.

However, there are a few commercial suppliers of prairie seed that have done a great disservice to the movement, misleading newcomers and some state agencies by maintaining that its perfectly acceptable to use seed from distant regions. Their argument is, quite simply, that it is not practical to use local seed. They maintain there is not enough local ecotype seed available, or it is too expensive. In fact, they use large volumes, can buy wholesale more cheaply from western producers, and make more money in the resale of these inappropriate varieties. They also make being a purist sound like an extremist approach taken by only a few. Limited availability may have been a problem initially but not today. If done properly, it takes only three years for a stand of the larger grasses to be harvestable for commercial sale of seed. More than two decades of restoration with local ecotypes have amply proved the vigor and suitability of local genetic varieties.

The sad result of the non-purist approach is that considerable quantities of western varieties of big bluestem, Indian grass, switch grass, and little bluestem have been planted in the Midwest, particularly on interstate and local road right-of-ways. This has happened because several state departments of transportation have been misled or were simply not aware of the problem and the options available. State and federal agencies, such as departments of conservation, departments of natural resources and the Fish and Wildlife Service that have insisted on local ecotypes on state parks, state wildlife areas, and federal refuges are to be commended.

It is not too late to take a stand. I urge anyone involved in prairie establishment to use reasonably local seed. Grass seed varieties are the worst problem. Frequently, beginning restorationists are not aware that many of the named varieties or strains of big bluestem, Indian grass, little bluestem, and switch grass, which are readily available in large quantities from the big seed producers of Kansas, Nebraska and Missouri, were selected and developed by the Soil Conservation Service and originated in the southern Great Plains. Since they are proven, vigorous varieties, they do well in the Midwest, but they are quite different from strains that evolved here and, in the minds of many, are not appropriate for use here. Contrary to what some might have us believe, for natural ecosystems, we really cannot improve on local natural selection.

And how local is local? I am not an extremist about local limits. As I stated in an earlier paper (Schramm 1978), two hundred miles is a reasonable distance to work within, but east-west rainfall regimes are a better guideline. For instance, western Illinois seed would not be appropriate for western Iowa, but it would be for western Indiana. Undoubtedly, in the original, vast, contiguous tracts of prairie, seeds of many species were dispersed great distances by animal fur, feathers, and droppings and by wind. The tiny postage stamp remnant gene pools left today were once part of a more connected genetic system. Thus, the case can be made for mixing prairie clover seed from a remnant in Chicago with prairie clover seed from Springfield and planting them with local seeds in a new restoration in Peoria. By working within reasonable distance limits in similar climatic regimes, we can preserve local genes and also do some mixing to maintain or recreate the genetic variety that must have been present in the original prairie.

THE MONOCULTURAL SWITCH GRASS SYNDROME

There has been a disturbing development in some areas of the Midwest, particularly in Iowa and Missouri, where projects are proclaimed to be prairie projects but are primarily monocultural stands of switch grass (*Panicum virgatum*). Somehow, the idea that big bluestem and Indian grass are difficult or slow to establish has resulted in excessive use of switch grass. It is quick and easy, but a closed, monocultural community with no diversity is exactly what we were trying to get away from when we turned to the natives. These stands have none of the positive attributes of the original prairie and are not even reasonable prairie facsimiles. For wildlife managers who have had good success with switch grass as roosting cover, I have observed that pheasants and quail prefer mixed stands of big bluestem and Indian grass to switch grass for winter roosting cover.

ROADSIDE PRAIRIES

Planting prairies along roadsides is finally becoming accepted. Long before the commercial people even knew about prairie, prairie biologists had been saying that prairie vegetation is a natural for roadsides. Low maintenance, erosion control, wildlife cover, beauty, and permanence, all contribute to its suitability. Unfortunately, people newly involved in this transformation are making many of the same mistakes that other new restorationist have been making. This is not an area for experimentation. Weedy failures on public land, there for everyone to see, are the worst kind of public relations for prairie restoration. Plead with all those involved in roadside management: "If you are going to do a prairie, do it correctly!"

Burning On Roadsides

First, be prepared to burn. Like all restorations, roadside prairies must be burned if they are to succeed and flourish. Without burning, the result is a weedy mess that will not get better with time. Such abortive attempts not only give prairie a bad name, but are a waste of the taxpayers' dollars. To be sure, there are a few prairie stands, mostly grasses, that have been established on roadsides without fire, mainly on sites where the worst possible subsoil provided a low-nutrient medium where non-prairie plants cannot compete. In the absence of competition from non-prairie weeds, the prairie plants succeeded. But even these stands could have been much better and would have developed much more rapidly with the proper use of fire.

The concern for public safety and traffic control during the burn and smoky conditions is a valid one. However, traffic is slowed and diverted regularly for repairs on roadways, sometimes for extended periods. Roadside burns need only brief periods of traffic control. Appropriate legislation and public education may be needed to clarify liability matters and to set the scene for safe fire management. These have been worked out for road repairs, and the same can be done for burning.

Planting Mixes For Roadsides

As in all other aspects of roadside restorations, an approach should be taken that is sure to succeed. This means use species and seed in the planting mix that are sure to successfully establish in a reasonably short period of time. A new restorationist may see a native stand of little bluestem growing on a steep road bank out in the country and conclude that that is the species to use in a comparable site on a new freeway. The problem is that little bluestem is very slow to establish; much more so than, say Indian grass. That country road bank stand may have been there for fifty or more years. A better approach would be to use the taller, more easily established grasses as the basic mix with a liberal amount of little bluestem thrown in. In time, it will contribute substantially to the overall, long-term stabilization of the new road bank site.

Roadside mixes should contain substantial amounts of the large grasses—by this we mean big bluestem and Indian grass. We know these species, if done properly, will grow on almost any site. Indian grass particularly, is an ideal grass for roadsides. It is slightly more xeric adapted than big bluestem. It establishes and flowers just a little bit faster and is an excellent choice for road banks, even steep ones. An all-purpose, ideal grass mix, pure live seed, for roadsides contains 60% Indian grass, 25% big bluestem, 10% little bluestem, and 5% switch grass. Another good basic road mix is 40% Indian grass, 40% big bluestem, 15% little bluestem, 5% switch grass. Or the switch grass can be left out entirely with no harm done. If it is included, use very sparingly.

Forb mixes for roadsides, like the grasses, should include species known to do well, such as the dominant species of Stages II and III. The more competitive and staying-power forbs can be included in the grass mixes to increase diversity. Mosaic planting can be done in cloverleafs and rest areas to assure a showy flower display.

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BAS

NATIVE FORB ESTABLISHMENT AND PERSISTENCE IN A GRASS-FORB SEEDING IN THE SOUTHERN PLAINS

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Abstract. Establishment of forbs in addition to grasses on marginal farmland in the Southern Plains can enhance wildlife habitat; improve forage quality; and, if legumes are used, fix nitrogen. This study explored establishment, herbage production, and persistence under grazing of five native forbs in northwestern Oklahoma. Purple prairie clover (*Dalea purpurea* Vent.), Illinois bundleflower (*Desmanthus illinoisensis* (Michx.) MacM.), scarlet pea (*Indigofera miniata* Ort.), partridge pea (*Cassia chamaecrista* L.), maximilian sunflower (*Helianthus maximilianii* Schrad.), and native grasses were drilled into a firm seedbed remaining after wheat (*Triticum aestivum* L.) was intensively grazed by cattle. Establishment of forbs and grasses was good, with an average of 1 plant established per 10 pure live seeds planted. The seeded forbs produced 33, 107, and 71 g m^{-2} representing 15, 29, and 36% of the herbage in the planting during the second, third, and fourth growing seasons, respectively. In June, grazing by steers was negligible on purple prairie clover and partridge pea, heavy on Illinois bundleflower, moderate on maximilian sunflower, and light to heavy on scarlet pea.

INTRODUCTION

Plowing of mixed- and shortgrass prairie in the Southern Plains began about 100 years ago. Extended drought, clean tillage practices, overgrazing, and high seasonal winds produced the great dust storms of the 1930s. The most severe wind erosion occurred in the Oklahoma panhandle and adjacent areas of adjoining states. Though not as spectacular, water erosion also was, and is, a major problem in the Southern Plains. Since the 1930s, establishment of grasses on eroded, marginal farmland has been a major part of conservation programs.

Establishment of forbs along with grasses would add diversity, thereby enhancing wildlife habitat (Schramm et al. 1987). Forbs could also improve forage quality and, if legumes were used, fix nitrogen in these plantings (Mauldin et al. 1988). However, forbs are not routinely seeded with native grass mixtures because 1) of added expense for forb seed, 2) seeding forbs precludes use of certain herbicides to control broadleaf weeds, and 3) information is sparse on establishment, benefits, and management of specific forb species.

Major contributors to knowledge on native forbs are the U.S. Department of Agriculture-Soil Conservation Service (SCS) Plant Materials Centers in Knox City, Texas; Manhattan, Kansas; and Los Lunas, New Mexico. These centers have screened many species and selections within species. Outstanding selections are released as named cultivars, and limited quantities of seed of promising, unreleased selections are made available to cooperators for field evaluation. Plant-available nitrogen is usually deficient in Southern Plains farmland as a result of 50 to 100 years of cropping and erosion. Thus, interest in native legumes has been long-standing (Kneebone 1959, Berg 1986, Maulden et al. 1988).

The objective of this paper is to document density, herbage production, and persistence under grazing of five forbs seeded in a mixture with six native grasses commonly planted on the Southern Plains. The forbs are selections that have generally proven outstanding in testing by SCS plant materials centers and others. This research is one segment of a regional study on land use effects upon runoff and associated soil and nutrient losses.

STUDY AREA AND METHODS

The study area is in northwestern Oklahoma on loamy upland soils (Woodward and Quinlan series; thermic Typic Ustochrepts). These soils, on 5 to 8% slopes, are typical of extensive areas of highly erodible soils on class IV land farmed to wheat (*Triticum aestivum* L.) in the Southern Plains. The soils are calcareous at or near the surface (pH near 8). They test low in nitrate nitrogen and adequate in plant-available P and K.

Long-term average annual precipitation on the area is 600 mm. Periodic, short-term drought is common, with wide yearly fluctuations in precipitation. About 70% of the precipitation is normally received during the frost-free period of mid-April to mid-October. The mean annual temperature is about 15 C with an expected yearly range of -18 to 40 C. Winds with gusts reaching 30 to 50 km/hr are common in the spring.

Under moderate grazing, native vegetation on loamy soils is usually dominated by a mixture of short, mid, and tall warm-season grasses. The grasses include blue grama (*Bouteloua gracilis* (H.B.K.)Lang. ex Griffiths), sideoats grama (*B. curtipendula* (Michx.) Torr.), little bluestem *(Andropogon scoparius* Michx.), sand bluestem (*Andropogon hallii* Hack.), switchgrass (*Panicum virgatum* L.), and Indian grass (*Sorghastrum nutans* (L.) Nash). Nomenclature follows Great Plains Flora Association (1986).

Local abundance of the warm-season forbs used in this study include purple prairie clover (*Dalea purpurea* Vent.), occasional on loamy upland sites; Illinois bundleflower *Desmanthus illinoensis* (Michx.) MacM.) and maximilian sunflower (*Helianthus maximilianii* Schrad.), occasional to common on moist sites protected from grazing; scarlet pea (*Indigofera miniata* Ort. var. *leptosepala* (Nutt.) B.L. Turner); and showy partridge pea (*Cassia chamaecrista* L.), occasional on upland sites and can be locally abundant on disturbed sites.

The area seeded to the native species mixture is a 3-ha gauged watershed previously farmed to wheat. The field was native range until plowed in 1979. A firm seedbed was developed by grazing wheat until mid-March 1987, allowing 10 days of wheat regrowth and then spraying with glyphosate.

In early April, a mixture of purple prairie clover *Kaneb*, Illinois bundleflower accession 421302, scarlet pea accession 477963, partridge pea *Comanche*, and maximilian sunflower *Prairie Gold* were drilled into the residue. Seeding was through the legume box of a Tye grassland drill equipped with double disc furrow openers and 1.5-cm depth bands. Spacing between rows was 25 cm. Each legume was inoculated with specific *Rhizobium* supplied by the Nitragin company. The legumes were not scarified. The following grasses were then drilled at a slight angle to the forb rows: blue grama *Hachita*, sideoats grama *El Reno*, little bluestem *Cimarron*, sand bluestem *Woodward*, switchgrass *Blackwell*, and Indian grass *Cheyenne*. Seeding rates (Table 1) suggested by SCS plant materials specialists were used for all species. Control of annual weeds was by flash grazing in early June and one mowing in late June.

Forb density was determined in July 1987 by identifying and counting each plant within 200 random placements of a 0.1 m^2 quadrat. Forb density was determined in June of 1988 and 1989 by 200 random placements of a 0.5 m^2 quadrat and in 1990 by 400 placements of a 0.5 m^2 quadrat. Grass species' density was determined each year using 100 placements of a 0.1 m^2 quadrat.

Herbage production at estimated peak standing crop (early July) was determined in 1988 by clipping forty 1/2 m^2 quadrats at ground level, separating species, oven drying, and weighing. Because the planting was grazed in 1989 and 1990, ten 3 x 3 m exclosures were randomly placed in the field and relocated each year. A 2-m^2 quadrat was sampled within each exclosure in 1989. In 1990, a 4-m^2 quadrat was sampled for grasses and purple prairie clover, and 9-m^2 was sampled for the other forbs within each exclosure.

The planting was grazed with yearling steers (180-270 kg) in April 1988 (50 steer days/ha), 7 to 27 June 1989 (110 steer days/ha), and 13 June to 2 July 1990 (80 steer days/ha). Standing dead vegetation was grazed in January and February of 1989 and 1990 with a stocking of 250 steer days/ha each year.

Precipitation in 1987, the year of seedling establishment, was 743 mm; this is 143 mm greater than the long-term average. Precipitation in 1988, 1989, and 1990 was 584, 623, and 361 mm, respectively.

Table 1. Forb and grass seeding rate, percent establishment, and density.

Species	*Seeding rate*	*Established*	*Density*			
			1987	*1988*	*1989*	*1990*
	pls†/m^2	%	plants/m^2			
Purple prairie clover	10	8	0.8	1.3	1.6	1.5
Illinois bundleflower	2	15	0.3	0.14	0.11	0.09
Scarlet pea	4	25	1.0	1.1	0.9	0.7
Partridge pea	8	16	1.3	6.2	¥	¥
Maximilian sunflower	0.5	40	0.2	0.1	0.3	0.3
Blue grama	30	23	7	8	8	6
Sideoats grama	30	33	10	16	1.4	1.4
Little bluestem	30	10	3	4	4	4
Sand bluestem	12	§	§	1.3	1.5	1.3
Switchgrass	20	10	2	2.0	2.8	2.4
Indiangrass	20	§	§	0.8	1.1	1.5

† Pure live seed.

¥ Not counted, annual species, many seedlings found some very small.

§ Sand bluestem and Indian grass seedlings not differentiated.

RESULTS AND DISCUSSION

Establishment

By mid-May, following planting in early April 1987, grass seedlings were abundant, and scattered forbs were present. A two-week rainy period (20 cm pptn.) started May 19, followed by timely rains of 2 to 3 cm/week through mid-July. Percent establishment ([number of seedlings/m^2 July 1987 : number of pure live seeds/m^2 planted in April 1987] x 100) ranged from 8% for purple prairie clover to 40% for maximilian sunflower (Table 1). This is excellent establishment for this region and is apparently a reflection of timely rains and a firm seedbed.

Many of the seedlings were 10 to 20 cm tall by mid-July. A few blue grama and sideoats grama plants were producing seedheads, and a few purple prairie clover, Illinois bundleflower, and partridge pea were blooming. Nodules with pink to dark red interiors were found on five of five partridge pea, four of five scarlet pea, two of five bundleflower, and one of five purple prairie clover plants when dug on July 20. The soil was moist but not highly friable when plants were dug; so some nodules may have been pulled off and, thus, not observed.

Observations on Grazing

Grazing during the 1989 and 1990 growing seasons commenced when there was 20 to 30 cm of new growth on the tall grasses (early to mid-June). At that time, purple prairie clover, Illinois bundleflower, and maximilian sunflower were also about 30 cm tall, and prairie clover was starting to bloom.

Grazing by steers was managed so that about half the grass biomass was consumed. At this grazing intensity and season of use, purple prairie clover was not grazed. Illinois bundleflower was heavily grazed. Maximilian sunflower was not grazed initially, but flower buds were heavily grazed as they emerged above the rosette of basal leaves. Only a few tips of scarlet pea and partridge pea were grazed in 1989. However, scarlet pea was heavily grazed in 1990.

Heavy grazing on maximilian sunflower was observed in April 1988 when the planting was grazed to control scattered, volunteer yellow sweet clover (*Melilotus officinalis*(L.)Pall). At that time, sunflower leaves were 8 to 10 cm long, warm-season grass shoots were 1 to 3 cm long, and the other warm-season forbs had not started top growth.

Literature (Johnson and Nichols 1970, Wasser 1982, Great Plains Flora Association 1986) generally indicates that purple prairie clover, Illinois bundleflower, and maximilian sunflower will decrease under heavy grazing. The grazing experience on this planting suggests that this will occur under yearly early-season grazing (April and May in Oklahoma). Under management based on moderate grazing (graze about 1/2 of grass biomass) of warm-season grasses in June and early July, it appears that purple prairie clover will not be grazed, Illinois bundleflower will be heavily grazed, and maximilian sunflower (buds) moderately grazed.

Gain of steers grazing the planting in June 1989 was 1.1 ± 0.06 (std. error) kg/day/steer and 120 kg/ha. Gain over the period June 13-July 2, 1990, was 1.5 ± 0.1 kg/day/steer and 125 kg/ha. These gains are similar to or somewhat greater than gains expected on good condition native range in the area and probably are a reflection of the vigor of the young stand and the relatively high fertility of the field. Total herbage yield calculated from data in Table 1 ranged from 2000 to 3700 kg/ha/yr. These yields are within the range estimated for the SCS loamy prairie range site in western Oklahoma (Cole et al. 1966). The fertility of many old fields farmed 70 to 100 years is considerably lower than this field that was farmed for eight years before being seeded to the native mixture.

Forb Performance

Purple prairie clover.

Purple prairie clover, with a density of 1 to 2 plants/m^2, was the most abundant forb (Table 1) and contributed substantially to herbage production (Table 2). Density increased from the first to the second growing season, probably due to germination of initially dormant seed.

When blooming in June, this density of purple prairie clover is striking against a background dominated by warm-season grasses. One can speculate that the density in this study is adequate for small wildlife use; however, quantitative data are needed. The unpalatability to cattle later in the growing season may be an advantage or disadvantage. Field data are needed to quantify the N_2-fixing potential on N-deficient soils. If it is a good N_2 fixer, greater density may be desirable, and the limited palatability may be an advantage.

Illinois bundleflower.

Illinois bundleflower had good initial establishment, but density decreased over the four growing seasons (Table 1), probably in response to grazing and competition. From the grazing and wildlife (Schramm et al. 1987) aspects, bundleflower may be the most desirable forb planted in this study. However, it appears that excellent grazing management will be required to maintain this species in a mixed planting.

Table 2. Herbage production by species in July 1988, 1989, and 1990.

	Herbage harvested in July, g/m²		
Species	*1988*	*1989*	*1990*
Purple prairie clover	13	34	54
Illinois bundleflower	5	15	2
Scarlet pea	9	15	3
Partridge pea	T†	33	T
Maximilian sunflower	6	10	12
Blue grama	20	25	55
Sideoats grama	67	130	
Little bluestem	16	40	34
Sand bluestem and Indian grass	23	24	19
Switchgrass	23	26	18
Other species	33	17	3

†T=trace.

Scarlet pea.

Scarlet pea established well and persisted in this planting (Table 1). It was very lightly grazed in 1989 and heavily grazed in 1990. Grazing in 1990 may have been as an alternative to grazing drought-stressed grass. This species has shown the ability to spread on N-deficient soils (Berg 1986), making it a candidate for use on infertile eroded sites.

Showy partridge pea.

Showy partridge pea, an annual, established well and produced seed abundantly the year initially seeded. Its density and herbage production (Tables 1 and 2) in ensuing years was highly dependent upon rain received in June and July. The yellow flowers have high aesthetic appeal. Steers did not graze this species when other herbage was readily available. Many small nodules were found on partridge pea roots in this study.

Maximilian sunflower.

Maximilian sunflower established readily (Table 1) and produced flowers the first growing season. It persisted well despite being the first species in the mixture to wilt and have leaves dry up from drought. Thus, it may not persist on upland sites in this area under extended drought. Numerous maximilian sunflower seedlings emerged in the spring of 1990, the fourth growing season; these are not included in the density recorded in Table 1.

OUTLOOK

"You mean we're going to plant weeds with grass?" was a farmer's reaction to a slide presentation on this grass-forb planting. This skeptically phrased question indicates that benefits of including native forbs in seeding mixtures will have to be proved and demonstrated before being accepted by many farmers and ranchers.

Many questions need to be answered—including the following: Will cattle (sheep, goats, etc.) graze this forb? If so, when, and how much? What is the forage quality? What management is needed to maintain this forb in a grass-forb planting? What are the wildlife values? What density is optimum for quail (or other wildlife)? What management is needed to optimize domestic grazing and wildlife values? What techniques can be used to establish forbs in existing grass stands (Dovel et al. 1989)? What is the nitrogen-fixing potential of the legumes?

This study and plantings by conservation agencies illustrate that selected forbs can be established with grasses on marginal farmland in the Southern Plains. Quantifying benefits from forbs and the grazing management needed to maintain forbs now appears to be the next step.

ACKNOWLEDGMENTS

I thank Soil Conservation Service Plant Material Centers' personnel for providing seed for this study. The work of John Loch in drilling, vegetation analysis, and grazing management is gratefully acknowledged.

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QUANTITATIVE TRENDS IN PROGRESSION TOWARD A PRAIRIE STATE BY SEED BROADCAST AND SEEDLING TRANSPLANT METHODS

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Abstract. A 0.63 ha area at a College of DuPage Prairie Restoration site was planted with 28 prairie species using two restoration methods: seed broadcast and seedling transplant. The Wilhelm Assessment Method was used to compare vegetational changes for these two methods in the absence of weed removal and fire during this four-year study. To record vegetational changes, plant species were identified and tallied along a 0.5 m wide transect for 21 north-south lines. The transects were 10 m apart and varied in length form 3.8 to 55.2 m. A seed broadcast area of 196.7 m^2 and a seedling transplant area of 42.7 m^2 were sampled for four years. There was a slow and steady decline in number and percent coverage of weed species (numerical rating < 4) and an increase in the percent coverage of prairie species (numerical rating ≥ 4) for both methods of restoration. The rating indices for both planting methods consistently increased. There were no significant differences ($p > .05$) between the restoration treatments during this four-year study. Progression toward a prairie state can be achieved by either seed broadcast or seedling transplant methods.

INTRODUCTION

The reestablishment of prairie species by seeding or transplanting on areas where the original vegetation was completely removed has been accomplished in several areas of the United States (Dale and Smith 1983). Prairie restorationists and researchers have reported the success of native prairie restoration in the Midwest (Anderson and Cottam 1970, Becic and Bragg 1978, Harper 1983, Schulenberg 1970, Sperry 1983). Most assessment analyses of prairie restoration or reconstruction sites have been qualitative, that is, good or poor, and not in terms of consistent standards (see Harper 1983, Sperry 1983).

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

This study compares quantitatively the vegetational changes in a seed broadcast area with those in a seedling transplant area in the absence of weed removal and fire. Quantitative analysis was accomplished using the Wilhelm Assessment Method (Swink and Wilhelm 1979, Wilhelm and Ladd 1988).

SITE LOCATION AND DESCRIPTION OF STUDY AREA

The study site is immediately north of a marsh on the campus of the College of DuPage in Glen Ellyn, Illinois: SW of NE Quarter, Sections 26 and 27, Township 39, Range 10 in DuPage County, Illinois. The study area of 0.63 ha is roughly rectangular in shape (Figure 1). Approximately one-half of the site is bordered by a thick stand of cattails (*Typha latifolia* L. and *T. angustifolia* L.) and sandbar willow (*Salix interior* Rowlee) on the south side and lawn grass on the north side.

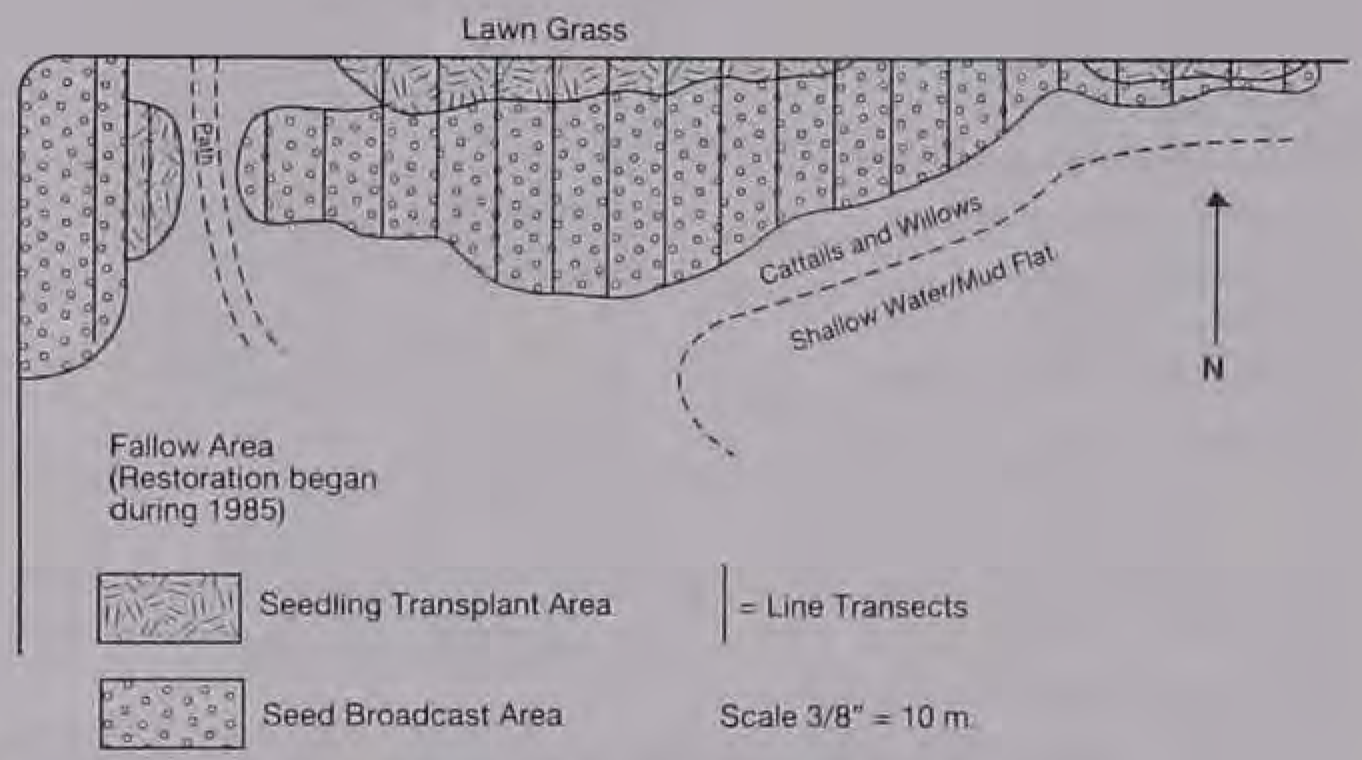

Figure 1. College of DuPage Prairie Restoration Area.

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

MATERIALS AND METHODS

All seeds were collected during 1983 from sites within a 40 km radius of the College of DuPage to ensure local genotypes. They were kept in cold storage until early February 1984. The seeds were

Table 1. Site soil characteristics.

Soil ph	8.0		*PPM*
Organic matter	3.57%	Zn	80.21
		B	58.00
		Mn	783.47
Kg/ha		Fe	28,627.33
		Cu	15.41
P	7.49	Al	23,185.00
K	207.76	Na	<69.49
Cation percent			
P	0.06		
K	0.60		
Ca	3.76		
Mg	2.30		
S	0.26		

The soil data is a composite of three random samples. It was analyzed by Department of Soil Science, University of Wisconsin Extension, Madison, Wisconsin 53705-4364.

Table 2. Seedlings of prairie species planted in seedling transplant area during spring, 1984. Nomenclature is from Swink and Wilhelm (1979).

Species	*Rating index*	*Number of seedlings*
Amorpha canescens	10	144
Baptisia leucantha	8	72
B. leucophaea	15	144
Coreopsis palmata	8	357
Echinacea pallida	8	251
Eryngium yuccifolium	9	196
Liatris pycnostachya	6	306
Parthenium integrifolium	7	288
Penstemon digitalis	4	23
Petalostemum candidum	15	681
P. purpureum	9	144
Potentilla arguta	9	36
Solidago rigida	4	216
Sporobolus heterolepis	9	5,256
Verbena stricta	4	72

Table 3. Seeds of prairie species planted in seed broadcast area during spring, 1984. Nomenclature is from Swink and Wilhelm (1979).

Species	*Rating index*	*Weight in grams*
Amorpha canescens (including calyces)	10	863
Andropogon gerardi	4	7,037
A. scoparius	5	272
Coreopsis palmata	8	136
C. tripteris	5	341
Echinacea pallida	8	681
Eryngium yuccifolium	9	636
Lespedeza capitata	4	91
Parthenium integrifolium	7	318
Petalostemum candidum (including calyces)	15	182
P. purpureum (including calyces)	9	1,907
Potentilla arguta	9	36
Pycnanthemum virginianum	5	454
Ratibida pinnata	4	726
Rudbeckia hirta	1	204
Silphium laciniatum	5	1,907
S. perfoliatum	5	82
S. terebinthinaceum	5	341
Solidago rigida	4	772
Sorghastrum nutans	5	200
Spartina pectinata	4	590
Sporobolus heterolepis	9	341
Vernonia fasciculata	5	114
Veronicastrum virginicum	6	145

Note: Monarda fistulosa (Rating index 4) *Penstemon digitalis* (Rating index 4), and *Panicum virgatum* (Rating index 5) were not knowingly included in the seed broadcast mixture.

then stratified with fine damp sand and refrigerated at 4°C to duplicate winter conditions. Legumes were scarified and inoculated with their appropriate *Rhizobium*.

During early April 1984, seeds from 15 prairie species (Table 2) were planted into a 50-50 mixture of "Jiffy Mix" (Ball Seed Company) and sterilized black soil in the College of DuPage greenhouse. During early to mid-May 1984, the seedlings were transplanted to individual jiffy pots and, after a week, acclimatized outside in a semi-shaded area. During late May and early June 1984, the acclimatized seedlings were transplanted to the restoration site (Figure 1). The entire restoration site was disced to a depth of 5-8 cm to level off the soil and break up soil clumps prior to transplanting and seed broadcastsing.

A mixture of 24 prairie species (Table 3) were broadcast adjacent to the seedling transplant area (Figure 1) from mid-May to early June 1984. Seeds were broadcast, lightly raked into the soil, and then compacted into the soil with a lawn roller that weighed 90 kg.

Oat straw and wheat straw were lightly scattered over both the seed broadcast and seedling transplant areas to conserve soil moisture and protect the seedlings from direct sunlight. Both areas were irrigated until 1 July 1984 whenever rainfall was insufficient.

For both planting methods, mesic-xeric species were introduced on higher elevations and mesic-hydric species on lower elevations. Whenever possible, species associations as described by Swink and Wilhelm (1979) were planted together.

The choice of plantings was based on seed availability, seed germination and competitiveness (Schramm 1978, Schulenberg 1972), time and space available to grow and transplant seedlings, and overall aesthetics. Although some different species were planted in each area, there was no significant difference ($p>.05$) in their average numerical rating ($X^2 = 0.273$: Goodness of Fit, Zar 1984).

To record vegetational changes, 196.7 m^2 were sampled in the seed broadcast area, and 42.7m^2 were sampled in seedling transplant area. Plant species were identified and tallied along a 0.5 m wide transect for 21 north-south lines during October of 1984, 1985, 1986, and 1987 (Figure 1). Nomenclature is from Swink and Wilhelm (1979). Tillers were counted as one individual. The transects, 10 m apart and from 3.8 to 55.2 m in length, were permanently marked.

The analyses were completed from 1984 to 1987 at the College of DuPage Restoration Project in Glen Ellyn, Illinois. Quantitative analysis was accomplished using the Wilhelm Assessment Method (Swink and Wilhelm 1979, Wilhelm and Ladd 1988). Wilhelm's method was used because terms such as high quality are nebulous, at best. One person's significant may be another's exceptional, depending on different philosophical alignment or technical experience in the field of natural area assessment (Wilhelm and Ladd 1988). Thus, repeatable application of such an assessment system is problematic. Wilhelm adopted an assessment method for the Chicago region that is based on a complete list of the Chicago region flora. For each species, a numerical rating has been assigned. These ratings identify each taxon's relative autecological value with respect to all other taxa in the flora (Swink and Wilhelm 1979). Then, based on autecological values for the species, a rating index for the community is generated as follows:

$$I = \frac{R}{\sqrt{N}}$$, where I = Rating Index
R = the sum of the numerical ratings for all taxa recorded for the area, and
N = the number of recorded taxa.

RESULTS AND DISCUSSION

Table 4 lists the plant species found growing in the seed broadcast area from 1984 to 1987. There were 22 prairie species present with a numerical rating of 4 or above. Species with a numerical rating of 4 or above were considered as native tallgrass prairie species that belong to the prairie community (Kirt 1989, Voigt and Mohlenbrock 1978). The Rating Index from 1984 to 1987 increased from 13.79 to 18.39 (Table 4). Weed species coverage decreased from 74% during 1984 to 56% in 1987 while the coverage of prairie species increased from 26% to 44% during this four year period (Figure 2). The Rating Index increase and the decrease of weed species suggest that the seed broadcast restoration area is progressing toward a prairie state in the absence of weed removal and fire.

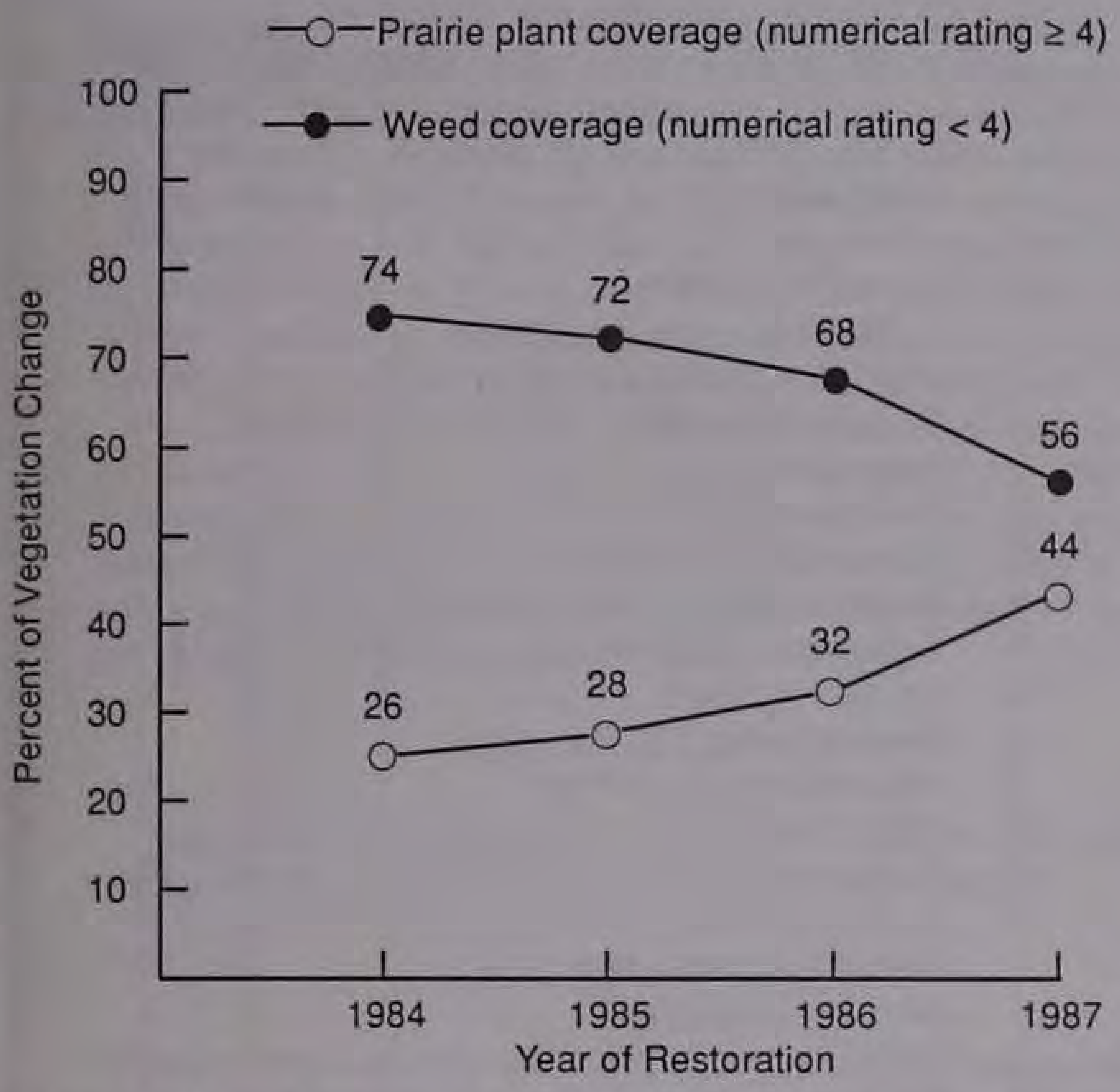

Figure 2. Percent of vegetation changes for plant species growing in seed broadcast area.

Table 4. Assignment of rating values and abundance of plant species in the seed broadcast area from 1984-87. Nomenclature is from Swink and Wilhelm (1979).

Numerical rating	*Recorded taxa*	*Number of plants*			
		1984	*1985*	*1986*	*1987*
-1	*Abutilon theophrasti*	110	109	3	0
0	*Acalypha rhomboidea*	6	3	2	1
-2	*Agropyron repens*	123	191	232	169
1	*Agrostis alba*	13	5	2	0
-1	*Amaranthus retroflexus*	16	0	5	0
0	*Ambrosia artemisiifolia*	193	1615	90	31
0	*A. trifida*	1	4	3	1
10	*Amorpha canescens*	4	7	29	38
4	*Andropogon gerardi*	541	791	638	662
0	*Anthemis cotula*	0	1	0	0
-3	*Arctium minus*	5	5	2	3
0	*Atrtplex patula*	16	4	0	0
4	*Aster novae-angliae*	0	0	0	3
1	*A. pilosus*	9	98	379	329
*	*Avena sativa*	298	0	0	0
1	*Barbarea vulgaris*	56	1	0	0
0	*Bidens sp.*	4	1	0	0
-1	*Brassica kaber*	37	0	0	0
-1	*Bromus inermis*	0	29	21	0
1	*Cerastium vulgatum*	12	0	8	0
1	*Chenopodium album*	284	107	1	1
1	*Cichorium intybus*	18	72	5	4
-3	*Votdoi, stbrmdr*	63	166	191	158
-3	*C. vulgare*	17	23	23	10
8	*Coreoposis palmata*	44	42	43	30
5	*C. tripteris*	281	313	218	172
1	*Cyperus strigosus*	*302*	76	0	0
1	*Dactylis glomerata*	2	0	7	9
1	*Daucus carota*	32	33	632	222
0	*Digitaria sanguinalis*	127	16	0	0
8	*Echinacea pallida*	98	103	86	61
0	*Echinochloa crusgalli*	252	6	3	0
0	*Erigeron canadensis*	0	43	9	1
9	*Eryngium yuccifolium*	8	7	9	15
-1	*Euphorbia supina*	33	0	8	0
1	*Festuca elatior*	20	24	4	5
2	*Helianthus grosseseratus*	0	3	2	0
0	*Hibiscus trionum*	76	119	17	0
-1	*Hordeum jubatum*	4	18	34	13
-1	*Lactuca scariola*	0	10	0	0
0	*Lepidium virginicum*	1	95	16	0
4	*Lespedeza capitata*	0	0	1	1
-2	*Lychnis alba*	0	17	0	0
-2	*Melilotus sp.*	7	0	0	2
4	*Monarda fistulosa*	0	1	3	0
-1	*Nepeta cataria*	4	2	0	0
0	*Oxalis stricta*	21	44	0	0
1	*Oenothera biennis*	0	1	1	0
1	*Panicum capillare*	40	5	2	0
5	*Panicum virgatum*	0	4	8	3
7	*Parthenium integrifolium*	18	4	8	5
-3	*Pastinaca sativa*	18	0	0	0
4	*Penstemon digitalis*	0	0	0	1
15	*Petalostemum candidum*	62	57	45	67
9	*P. purpureum*	102	78	131	110
1	*Phleum pratense*	0	4	6	0
0	*Plantago major*	132	233	55	51
0	*P. rugelii*	19	5	6	0
1	*Poa annua*	13	2	0	0
0	*P. pratensis*	108	267	204	180
0	*Polygonum pensylvanicum*	203	33	0	0
2	*Populus deltoides*	24	6	3	4
9	*Potentilla arguta*	1	8	6	4
0	*P. norvegica*	13	28	4	0
5	*Pycnanthemum virginianum*	6	5	2	2
4	*Ratibida pinnata*	496	573	314	254
5	*Rorippa islandica fernaldiana*	16	0	0	0
1	*Rudbeckia hirta*	134	136	30	28
-1	*Rumex crispus*	31	44	13	6
1	*Salix interior*	10	8	9	7
-1	*Setaria faberii*	116	11	1	0
0	*S. glauca*	299	38	4	2
-1	*S. viridis*	137	113	4	2
5	*Silphiulm laciniatum*	192	196	161	173
5	*S. perfoliatum*	19	18	28	13
-1	*Solanum americanum*	15	0	3	0
1	*Solidago altissima*	7	2	15	56
4	*S. rigida*	77	96	165	185
-2	*Sonchus uliginosus*	10	48	1	1
5	*Sorghastrum nutans*	24	41	51	58
5	*Spartina pectinata*	7	9	8	7
9	*Sporobolus heterolepis*	1	2	1	1
0	*Taraxacum officinale*	309	145	119	19
1	*Trifolium hybridum*	37	47	9	5
1	*T. pratense*	44	36	12	2
1	*T. repens*	52	31	90	1
-1	*Xanthium americanum*	1	1	0	0
N	(Number of recorded taxa)	72	72	66	50
I	(Rating Index)	13.79	15.32	16.37	18.39
*	No numerical rating				

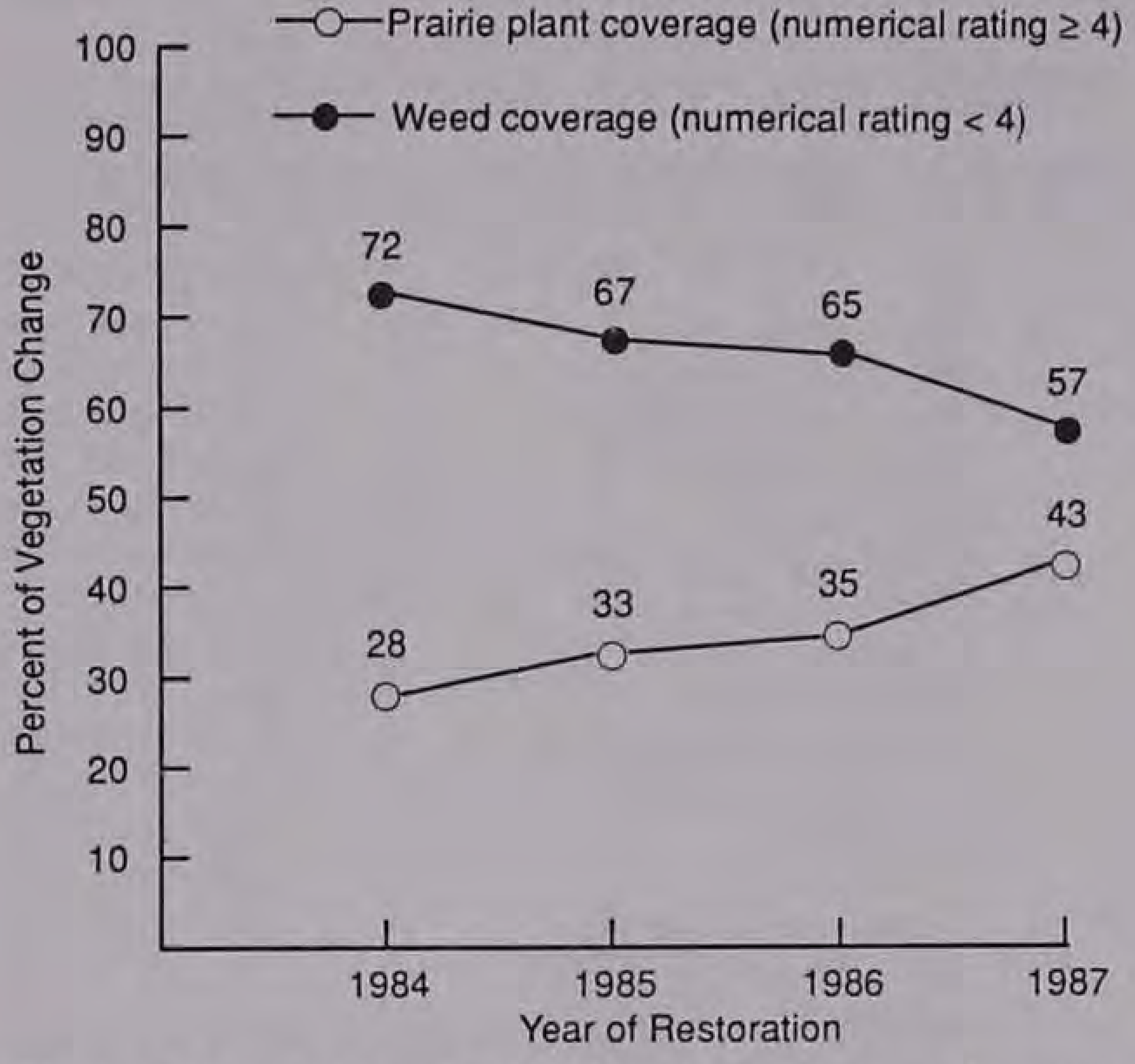

Figure 3. Percent of vegetation changes for plant species growing in seedling transplant area.

Table 5 lists the plant species found growing in the seedling transplant area from 1984 to 1987. During 1987, 19 prairie species with a numerical index of 4 or above were present in the seedling transplant area. Of these 19 species, big bluestem (*Andropogon gerardi* Vitman), New England aster (*Aster novae-angliae* L.), tall coreopsis (*Coreopsis tripteris* L.), and compass plant (*Silphium laciniatum* L.) germinated from seeds from the adjacent seed broadcast and marsh areas. The Rating Index from 1984 to 1987 increased from 14.29 to 20.83 (Table 5). Weed species coverage decreased from 72% to 57% while the coverage of prairie species increased from 28% to 43% during this four year period (Figure 3). This increase in Rating Index and decrease of weed species suggests that the seedling transplant area is also progressing toward a prairie state.

Table 5. Assignment of rating values and abundance of plant species in the seedling transplant area from 1984-87. Nomenclature is from Swink and Wilhelm (1979).

Numerical rating	*Recorded taxa*	*Number of plants*			
		1984	*1985*	*1986*	*1987*
-1	*Abutilon theophrasti*	21	40	3	0
0	*Acalypha rhomboidea*	0	1	0	0
-2	*Agropyron repens*	7	31	29	13
-1	*Amaranthus retroflexus*	8	0	0	0
0	*Ambrosia artemisiifolia*	23	428	85	22
10	*Amorpha canescens*	0	3	2	6
4	*Andropogon gerardi*[a]	3	5	1	1
0	*Anthemis cotula*	0	0	1	0
-3	*Arctium minus*	1	3	2	4
0	*Atriplex patula*	3	5	0	0
4	*Aster novae-angliae*	0	0	0	1
1	*A. pilosus*	0	4	30	65
*	*Avena sativa*	59	0	0	0
8	*Baptisia leucantha*	0	3	3	3
15	*B. leucophaea*	1	1	3	5
1	*Barbarea vulgaris*	14	1	0	0
-1	*Brassica kaber*	5	1	0	0
1	*Cerastium vulgatum*	8	0	0	0
1	*Chenopodium album*	89	17	0	0
1	*Cichorium intybus*	0	8	9	0
-3	*Cirsium arvense*	9	16	56	48
-3	*C. vulgare*	1	9	46	14
8	*Coreopsis palmata*	3	10	17	24
5	*C. tripteris*[a]	0	1	1	1
1	*Cyperus strigosus*	26	0	0	0
1	*Dactylis glomerata*	1	0	0	0
1	*Daucus carota*	8	16	267	122
8	*Echinacea pallida*	17	17	18	17
0	*Echinochloa crusgalli*	36	2	0	0
0	*Erigeron canadensis*	0	9	6	2
9	*Eryngium yuccifolium*	7	9	5	6
-1	*Euphorbia supina*	5	0	0	0
1	*Festuca elatior*	3	2	3	1
2	*Helianthus grosseseratus*	3	0	0	0
0	*Hibiscus trionum*	10	14	3	0
-1	*Hordeum jubatum*	0	5	23	9
-1	*Lactuca scariola*	0	1	0	0
0	*Lepidium virginicum*	1	2	2	0
6	*Liatris pycnostachya*	0	8	1	2
-2	*Lychnis alba*	0	0	0	1
-2	*Melilotus sp.*	1	1	1	0
0	*Oxalis stricta*	1	4	4	0
1	*Oenothera biennis*	0	0	3	4
7	*Parthenium integrifolium*	7	4	6	5
4	*Penstemon digitalis*	0	2	2	1
15	*Petalostemum candidum*	14	15	18	26
9	*P. purpureum*	6	14	18	23
1	*Phleum pratense*	0	0	1	0
0	*Plantago major*	8	14	6	18
0	*P. rugelii*	2	3	0	0
0	*Poa pratensis*	10	9	4	0
0	*Polygonum pensylvanicum*	11	5	0	0
2	*Populus deltoides*	11	3	3	1
9	*Potentilla arguta*	8	6	6	7
0	*P. norvegica*	3	2	2	0
4	*Ratibida pinnata*[a]	3	1	0	0
5	*Rorippa islandica fernaldiana*	2	0	0	0
1	*Rudbeckia hirta*[a]	1	1	13	4
-1	*Rumex crispus*	6	6	8	7
-1	*Setaria faberii*	19	0	2	0
0	*S. glauca*	61	33	6	0
-1	*S. viridis*	15	49	12	1
5	*Silphium laciniatum*[a]	1	3	1	1
-1	*Solanum americanum*	7	1	0	0
1	*Solidago altissima*	0	0	10	11
4	*S. rigida*	17	10	29	45
-2	*Sonchus uliginosus*	3	53	15	0
9	*Sporobolus heterolepis*	155	196	203	189
0	*Taraxacum officinale*	108	42	79	7
1	*Trifolium hybridum*	12	12	8	2
1	*T. pratense*	4	8	4	2
1	*T. repens*	11	7	58	9
1	*Verbascum thaspus*	4	4	2	1
4	*Verbena stricta*	1	1	1	1
-1	*Xanthium americanum*	0	0	0	2
N	(Number of recorded taxa)	54	58	52	42
I	(Rating Index)	14.29	17.46	18.31	20.83

[a] Seeds of *A. gerardi*, *C. tripteris*, *R. pinnata*, *R. hirta*, and *S. laciniatum* from seed broadcast mixture became established in seedling transplant area.

* No numerical rating

There was a slow but steady decline of weed species and consistent increase in coverage of native prairie species for both the seed broadcast and seedling transplant areas during the first four years of assessment. Weeds occurred spontaneously from the 7 to 10 cm of black soil used to top-dress the area, the clay and rubble subsoil, the adjacent marsh vegetation, and the oat and wheat straw mulch that was scattered on both the broadcast and transplant areas. Our results are similar to those reported by others (Dale and Smith 1983, Woehler and Martin 1983). Both restoration areas have progressed toward prairie states in the absence of weed removal and fire.

At the end of four years, the seedling transplant area contained 19 prairie species with an average numerical rating of 7.52. The seed broadcast area contained 22 prairie species with an average numerical rating of 6.50. After the first four years, neither restoration area was significantly different ($p>.05$) in the overall quality of prairie present ($X^2 = 0.074$: Goodness of Fit, Zar 1984).

ACKNOWLEDGEMENTS

Appreciation is expressed to Chris E. Petersen (College of DuPage) for his helpful comments and review of manuscript.

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ESTABLISHMENT AND MANAGEMENT OF A CAMPUS PRAIRIE DEMONSTRATION

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Abstract. In 1988, two prairie demonstration plots were established on the campus of Midland Lutheran College to provide research opportunities for undergraduate students, increased public awareness of prairie vegetation, and a study area for use by classes in science and in Great Plains studies. Twenty-nine species of potted seedlings, consisting of ten grasses and nineteen forbs, were planted 18-22 April 1988. An approximate 1:1 ratio of grasses to forbs was used. Management during the subsequent two growing seasons included a spring burn on 19 April 1989 and mowing with removal of clippings on 20 April 1990. Analysis by the line intercept method was utilized to determine changes in species distribution and the extent of invasion by plants not included in the original 1988 planting. A total of five graminoids, seven forbs, and four woody species not originally present were recorded. The tall grasses competed very successfully against invading species, but hairy crabgrass (*Digitaria sanguinalis* (L.) Scop.), common ragweed (*Ambrosia artemisiifolia* L.), and perennial ryegrass (*Lolium perenne* L.) occasionally crowded and shaded shorter species. Selective mowing and weeding of problem areas was used to assist in the establishment of native species.

INTRODUCTION

In 1988, the Peter Kiewit Foundation, administered by the Nebraska Statewide Arboretum, awarded Midland College a $15,000 matching grant. Although these funds were originally earmarked to purchase trees and shrubs for landscaping purposes, this grant presented an excellent opportunity to establish a campus prairie demonstration. Several original prairie remnants and restorations are located 8-16 km from the Midland Campus, but these sites are largely inaccessible to the Midland College Community and the general public. Midland College's location near the center of Fremont, Nebraska, guarantees easy public access to the demonstration prairie and was an important consideration in site selection. After an examination of the merits of this campus prairie project, the Midland College Campus Beautification Committee agreed to include the purchase of grasses and forbs as part of the landscaping project plan.

This paper reports procedures used and results obtained during the first two years of the project. The prairie demonstration was established in order to provide 1) an increased public awareness and appreciation of vegetation native to eastern Nebraska; 2) research opportunities for undergraduate students in ecology, botany, and general biology classes; and 3) a demonstration or teaching tool for use in Great Plains studies and science courses. With these objectives in mind, plant species were selected and a planting pattern was designed (see Methods) to create two prairie demonstration plots that would be both functional and aesthetically attractive. A management plan, incorporating alternate spring burning and mowing, was devised to encourage growth of desirable prairie plants and reduce growth of weedy invaders.

During the 1990 growing season, absolute and relative cover were obtained by the line intercept method using parallel lines run from permanent markers established along the edge of each plot. Data gathered from future growing seasons will indicate changes in species composition over time for comparison to the original planting pattern.

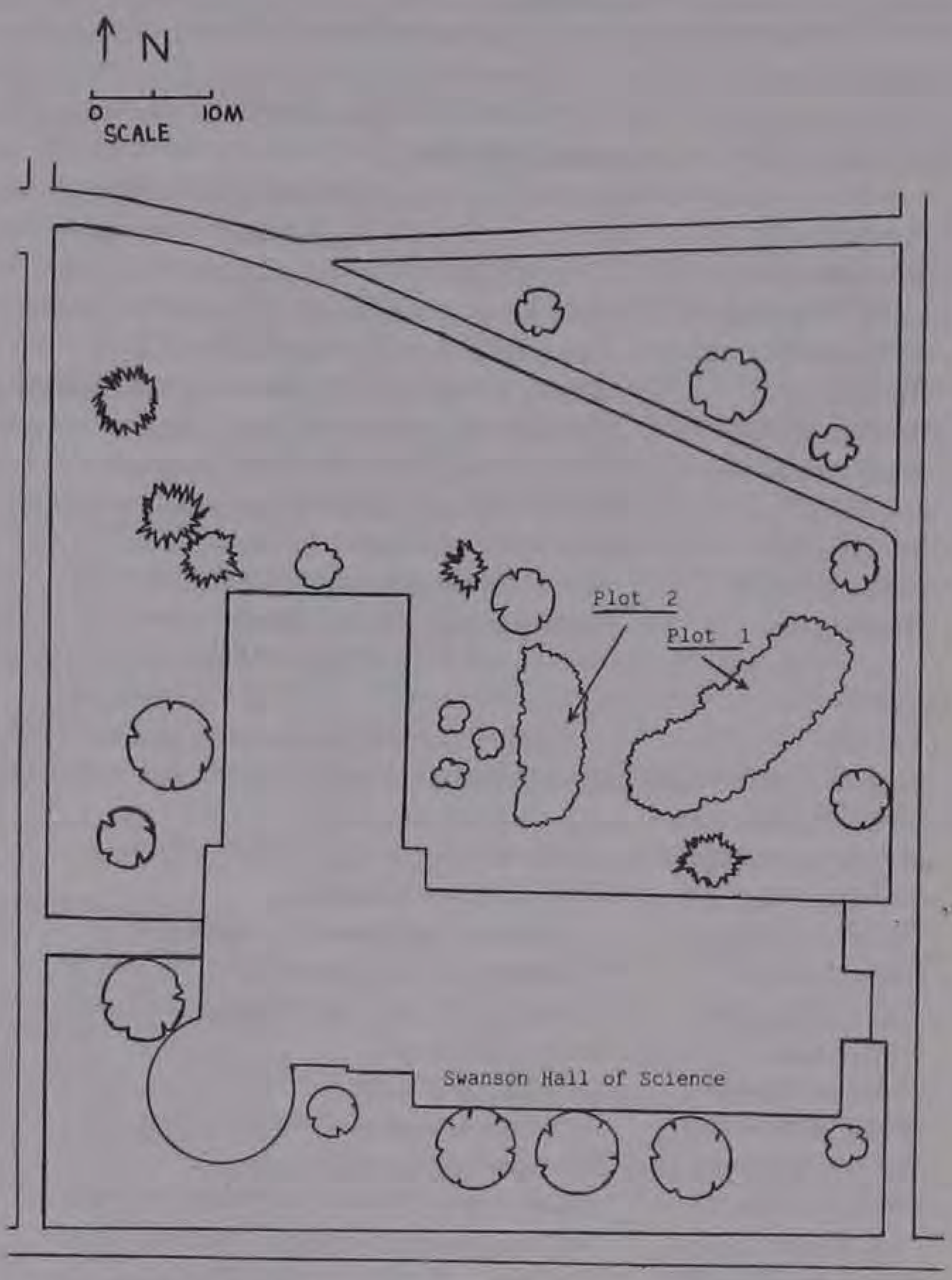

Figure 1. The relationship of demonstration plots 1 and 2 to the overall landscaping plan.

METHODS

Establishment

Twenty-nine species, consisting of 10 grasses and 19 forbs, were planted from 18 April to 22 April 1988 (Table 1). All plants were potted seedlings obtained from Bluebird Nursery Inc., Clarkson, Nebraska, 68629. The forbs included representative species that flower during spring, summer, late summer, and fall flowering periods. Water was applied to the seedlings when planted, and additional watering took place twice weekly for two weeks until the root systems were better established. The plants were place approximately 0.6 m (2 ft) apart, resulting in a density of 2.7 plants per m². Plot 1 measured approximately 20 x 8 m (160 m²), and Plot 2 measured 15 x 5 m (75 m²). Both demonstration plots were established on sloped surfaces created by addition of topsoil provided to the campus by a landscape construction company (Figure

1). The design reflected differences in species composition over a small-scale topographic gradient. Nomenclature for all species follows the Great Plains Flora Association (1986).

Originally, grasses and forbs were planted in a 1:1 ration. Additional buffalo grass (*Buchloe dactyloides* (Nutt.) Engelm.) seedlings were ordered and planted on 30 April 1988 in order to increase the density of plants bordering each planting.

Table 1. A list of forbs and grasses comprising the original prairie demonstration planting.

Species	
Common Name	*Scientific Name*
Grasses	
Big bluestem	*Andropogon gerardii* Vitman
Little bluestem	*Andropogon scoparius* Michx.
Side-oats grama	*Bouteloua curtipenula* (Michx.) Torr.
Blue grama	*Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths
Buffalo grass	*Buchloe dactyloides* (Nutt.) Engelm.
Sand lovegrass	*Eragrostis trichodes* (Nutt.) Englem.
Junegrass	*Koeleria pyramidata* (Lam.) Beauv.
Switchgrass	*Panicum virgatum* L.
Indian grass	*Sorghastrum nutans* (L.) Nash
Needlegrass	*Stipa comata* Trin. & Rupr.
Forbs	
Yarrow	*Achillea millefolium* L.
Butterfly milkweed	*Asclepias tuberosa* L.
New England aster	*Aster novae-angliae* L.
Purple poppy mallow	*Calliroe involucrata* (T.&G.) A.Gray
Shooting star	*Dodecatheon meadia* L.
Purple coneflower	*Echinacea purpurea* (L.) Moench.
Joe-pye weed	*Eupatorium purpureum* L.
Tall blazing star	*Liatris pycnostaycha* Michx.
Native flax	*Linum perenne* L.
Cardinal flower	*Lobelia cardinalis* L.
White penstemon	*Penstemon digitalis* Nutt. ex Sims
Shell-leaf penstemon	*Penstemon grandifloris* Nutt.
White prairie clover	*Petalostemon candidum* (Willd.) Michx.
Pink prairie clover	*Petalostemon purpureum* (Vent.) Rydb.
Prairie coneflower	*Ratibida columifera* (Nutt.) Woot. & Standl.
Black-eyed susan	*Rudbeckia hirta* L.
Rigid goldenrod	*Solidago rigida* L.
Spiderwort	*Tradescantia bracteata* Small.
Rose verbena	*Verbena canadensis* (L.) Britt.

Management

Both demonstration plots were burned on 19 April 1989 and mowed to a height of 20.3 cm (8 in) on 20 April 1990. Following the spring 1990 mowing, clippings, leaf litter, and other debris were removed by hand raking. During the 1989 and 1990 growing seasons, woody plants not killed by burning and large weeds were selectively cut or mowed to promote better establishment of native species. This selective removal of weedy species was not done systematically, but only in problem areas.

Plant analysis by the line intercept method (Mueller-Dombois and Ellenberg 1974) was begun during the summer of 1990 and will be repeated during subsequent growing seasons. Changes in species composition over time will then be available for comparison to the original planting pattern. Permanent markers were established at 1 m intervals along the edge of each plot to serve as reference points. Absolute cover for plant species was recorded along parallel lines spaced 1 m apart across each of the two plots. Absolute cover equaled the total intercept lengths in meters for each species. Data from each of the two plots were recorded separately and used to calculate relative cover values. Relative cover was calculated by the formula:

$$\text{Relative cover} = \frac{\text{total of intercept lengths for a species}}{\text{total of intercept lengths for all species}} \times 100$$

and is indicative of species importance at both plots (Tables 2 and 3).

Table 2. Absolute and relative cover for plants present in demonstration plot 1.

Species	*Absolute cover (m)*	*Relative cover (%)*
Graminoids		
Switchgrass, *Panicum virgatum* L.	7.3	11.5
Buffalo grass, *Buchloe dactyloides* (Nutt.) Engelm.	6.7	10.6
Hairy crabgrass, *Digitaria sanguinalis* (L.) Scop.	3.0	4.7
Indian grass, *Sorghastrum nutans* (L.) Nash	3.0	4.7
Yellow nutsedge, *Cyperus esculentus* L.	1.8	2.8
Witchgrass, *Panicum capillare* L.	1.1	1.7
Big bluestem, *Andropogon gerardii* Vitman	1.0	1.6
Perennial ryegrass, *Lolium perenne* L.	1.0	1.6
Yellow foxtail, *Setaria glauca* (L.) Beauv.	0.9	1.4
Forbs		
New England aster, *Aster novae-angliae* L.	12.3	19.4
Black-eyed susan, *Rudbeckia hirta* L.	7.4	11.7
Common ragweed, *Ambrosia artemisiifolia* L.	7.1	11.2
Joe-pye weed, *Eupatorium pupureum* L.	4.6	7.3
Spiderwort, *Tradescantia bracteata* Small	1.3	2.1
Prairie coneflower, *Ratibida columnifera* (Nutt.) Woot, & Standl	0.8	1.3
Wooly verbena, *Verbena stricta* Vent.	0.8	1.3
Western yarrow, *Achillia millefolium* L.	0.7	1.1
Redroot pigweed, *Amaranthus retroflexus* L.	0.6	0.9
Black nightshade, *Solanum interius* Rydb.	0.4	0.6
Horseweed, *Conyza canadensis* (L.) Cronq.	0.3	0.5
Green ash, *Fraxinus pennsylvanica* Marsh.	0.3	0.5
Purple poppy mallow, *Callirhoe involu crata* (T.&G.) A. Gray	0.2	0.3
White mulberry, *Morus alba* L.	0.2	0.3
American elm, *Ulmus americana* L.	0.2	0.3
Tall blazing star, *Liatris pycnostachya* Michx.	0.1	0.2
Rigid goldenrod, *Solidago rigida* L.	0.1	0.2
White Clover, *Trifolium repens* L.	0.1	0.2

RESULTS AND DISCUSSION

Overall, the plants became well established, and most species flowered during the first growing season. Heavy competition from common ragweed (*Ambrosia artemisiifolia* L.), hairy crabgrass (*Digitaria sanguinalis* (L.) Scop.), and yellow foxtail (*Setaria glauca* (L.) Beauv.) was localized to areas with shorter grasses and forbs.

Table 3. Absolute and relative cover for plants present in demonstration plot 2.

Species	*Absolute cover (m)*	*Relative cover (%)*
Graminoids		
Switchgrass, *Panicum virgatum* L.	7.6	29.3
Hairy crabgrass, *Digitaria sanguinalis* (L.) Scop.	2.0	7.7
Buffalo grass, *Buchloe dactyloides* (Nutt.) Engelm.	1.8	7.0
Big bluestem, *Andropogon gerardii* Vitman	1.5	5.8
Sand lovegrass, *Eragrostis trichodes* (Nutt.) Wood.	1.0	3.9
Perennial ryegrass, *Lolium perenne* L.	0.5	1.9
Forbs		
New England aster, *Aster novae-angliae* L.	3.9	15.1
Common ragweed, *Ambrosia artemisiifolia* L.	3.3	12.7
Prairie coneflower, *Ratibida columnifera* (Nutt.) Woot, & Standl	1.8	6.9
Purple coneflower, *Echinacea purpurea* (L.) Moench.	0.5	1.9
Wooly verbena, *Verbena stricta* Vent.	0.5	1.9
Purple poppy mallow, *Callirhoe involu crata* (T.&G.) A. Gray	0.4	1.5
Butterfly milkweekd, *Asclepias tuberosa* L.	0.3	1.2
White mulberry, *Morus alba* L.	0.2	0.8
Common ground cherry, *Physalis Longifolia* Nutt.	0.2	0.8
Spiderwort, *Tradescantia bracteata* Small	0.2	0.8
American vetch, *Vicia americana* Muhl. ex Willd.	0.2	0.8

Burning, grazing, or mowing with removal of plant clippings are desirable management strategies to remove excess plant litter that reduces productivity (Knapp and Seastedt 1986). By selectively mowing these problem areas at a height of 0.2 m (8 in), along with some weeding, the desired native species gradually became dominant. Taller plants that form dense stands, such as big bluestem (*Andropogon gerardii* Vitman), switchgrass (*Panicum virgatum* L.), Indian grass (*Sorghastrum nutans* (L.) Nash), New England aster (*Aster novae-angliae* L.), Joe-pye weed (*Eupatorium purpureum* L.), and purple coneflower (*Echinacea purpurea* (L.) Moench.) were very successful competing with invading species.

Regular spring burning is perhaps the most effective management method because it reduces competition from cool-season plants and woody species (Hulbert 1986). Schearer and Tiffany (1988) reported decreased frequencies of fungal foliar diseases on plants growing in burned versus unburned prairie plots. Other benefits resulting from fire are the stimulation of growth and flowering, delayed senescence, and increased soil warming, which is advantageous to warm-season species (Smith 1990). Various city and/or state laws can be a drawback to fire management, especially if the site is within the city limits. A permit was obtained for the Midland project, but it required an endorsement by the college administration, city council action, and permission from the Fremont Fire Department. Occasionally, restrictions placed on such permits can make frequent fire management very difficult.

At Midland, we have opted to burn the plots on an every-other-year basis, alternating with spring mowing and removal of clippings. This schedule may be altered (for example, every two out of three years) if more frequent burning is needed to inhibit the growth of weedy biennials. Less frequent or earlier burning and mowing may be used to encourage the growth of species that set seed early, such as Junegrass (*Koeleria pyramidata* (Lam) Beauv.) and needlegrass (*Stipa comata* Trin. & Rupr.). Depending on site location and local conditions, it is important to maintain a degree of flexibility with regard to a spring burning schedule. Optimum dates for spring burning vary with the latitude of the site, exposure (north or south facing), and altitude.

Factors considered when deciding on planting density were cost, time, labor, and availability of plant materials (Diekelmann 1986). All of these are directly related to the size of the planting. Shorter plants, such as buffalo grass, blue grama (*Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths), and little bluestem (*Andropogon scoparius* Michx.), are more typical of mixed-grass prairies (Weaver and Albertson 1956) and were planted along the higher, well-drained slopes of both plots. Taller species, such as big bluestem, Indian grass, and switchgrass, native to the eastern tallgrass prairie were placed on lower, more level sections of each site to simulate their native habitats (Figure 2). Because it spreads rapidly by creeping rhizomes, a border of buffalo grass was used in both plots to help reduce competition from perennial ryegrass (*Lolium perenne* L.), the dominant cool-season grass seeded on campus.

Species diversity is atypically high for such small plots, but this is desirable for demonstration or landscaping purposes. Grasses and forbs from the original planting were dominant, but there was a significant presence of several invaders: hairy crabgrass, common ragweed, and perennial ryegrass (Tables 2 and 3). Of the species used in the original planting, 50% of the grasses and 58% of the forbs were present in the line intercept analysis. Also, several other original grass and forb species were still present but in low num-

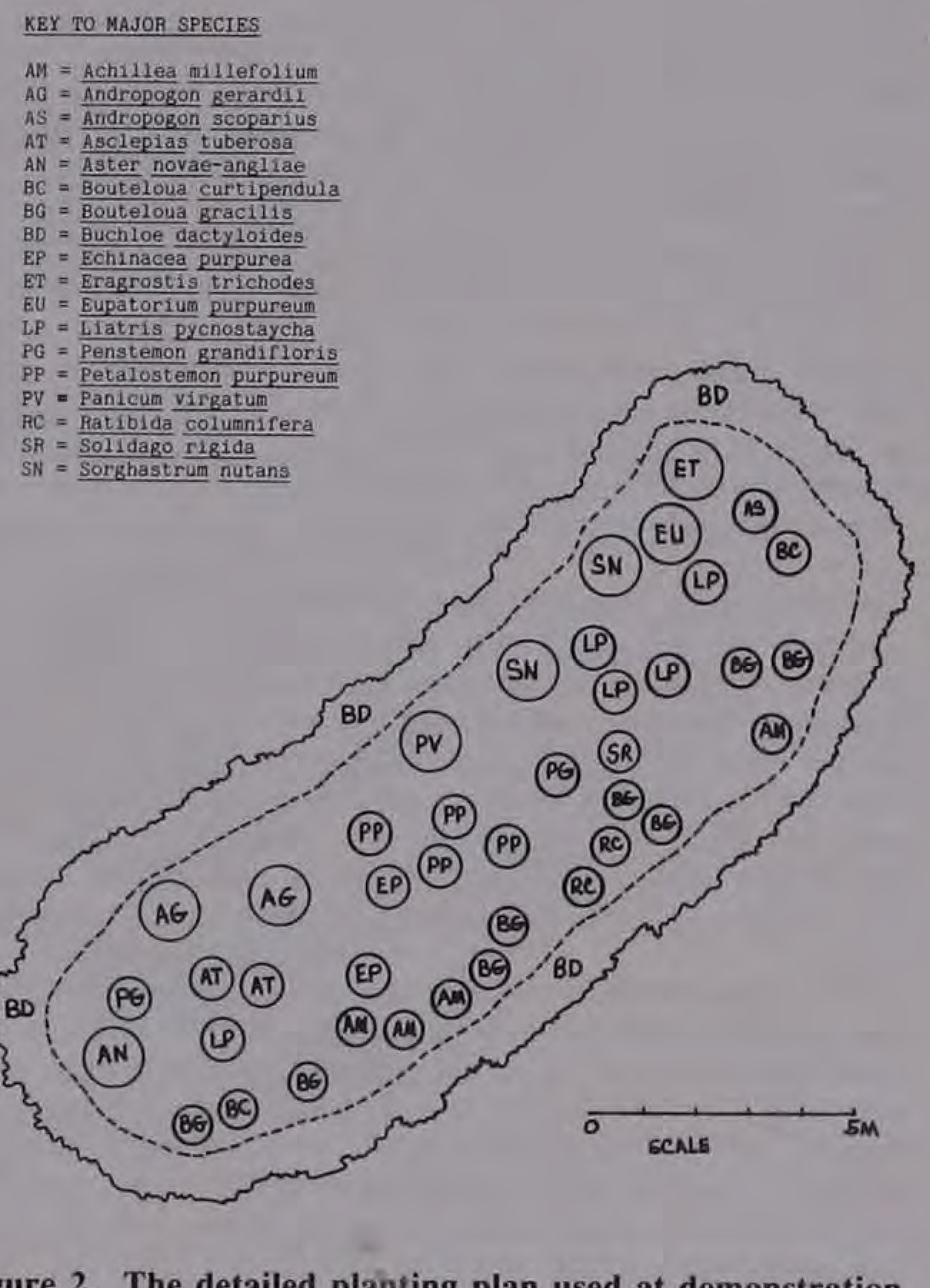

Figure 2. The detailed planting plan used at demonstration plot 1.

bers or in locations that prevented their inclusion in these data. A total of five grasses, seven forbs, and four woody species not originally present were recorded.

To date, the prairie restoration has been beneficial to a number of individuals, groups, and classes. These include local grade school and secondary school students, Midland students with special projects in biology and ecology, and an Elderhostel class studying the Great Plains. A printed brochure or guide to the prairie project is planned for the future.

A prairie demonstration or reconstruction is a developing system, constantly in flux. Competition among the native grasses and forbs and with weedy volunteers changes species distribution and composition. Frustrations caused by invading weedy species are offset by the many opportunities to participate in the development of a unique miniature ecosystem. The recognition and documentation of major or minor successional trends will be an important aspect of future studies.

ACKNOWLEDGMENTS

I am grateful to Bill Whitney of the Prairie Plains Resource Institute, Aurora, Nebraska, and to Richard Sutton, Department of Horticulture, University of Nebraska-Lincoln, for their advice and encouragement. Also, thanks to Paul Bookmeyer, Vice President for Finance at Midland College, for his help in making this project a reality.

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CULTURAL ADAPTATIONS TO THE PRAIRIE ENVIRONMENT: THE IOWAY EXAMPLE

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Abstract. The Ioway Indians offer an excellent example of American Indian adaptive strategies in the western prairie peninsula environment from A.D. 1250 to 1825. Using the methodology of cultural ecology, archeological, linguistic, ethnographic, historic and climatological data can be combined to define the adaptive measures employed by the Ioway and to explain their tribal movements through time.

INTRODUCTION

The Ioway Indians offer an excellent example of adaptation to environmental and cultural change in the western prairie peninsula. Judging from both archeological and linguistic evidence cited in the discussion, the Ioway had evolved as a tribal entity by no later than 1500 A.D., supporting themselves with a mixed economy based on hunting (principally bison); bottomlands gardening of corn, beans, squash and a few other domesticated plants; and fishing and collecting.

The Ioway did not always live in Iowa; they probably evolved in western Wisconsin. As bison availability increased west of the Mississippi during the Pacific climatic episode of 1100-1550 A.D., they moved across the river to take full advantage of this marvelous resource. From earliest historic contact, the Ioway appear to have been semi-nomadic due to several factors: l) shifting resource availability, 2) conflicts with their Native American neighbors, 3) efforts to develop and maintain favorable trading relationships with whites, and 4) attempts to develop and maintain peaceful alliances with other tribes. A small tribe, in contrast to several near neighbors, including the Dakota Sioux, Sauk and Fox, Osage and Pawnee, their attempts at independence and autonomy were futile; by 1830, the Ioway had ceded all claim to land in the present state of Iowa.

DISCUSSION

The archaeological remains of the Ioway are part of the Oneota cultural tradition. The Oneota Tradition dates from A.D. 1,000 into the historic contact period. It is generally defined within a Prairie Peninsula habitat (Borchert 1950) and is viewed as peninsula-based, although many Oneota sites are found in marginal, ecotonal loci. Oneota is the traditional culture of the Chiwere Sioux (Griffin 1937), including the Winnebago, Ioway, Oto, and Missouri Indians. Others who apparently assumed portions of the Oneota Tradition upon their arrival in the Prairie Peninsula are the Kansa, Omaha, Osage, and Miami. Data presented by Lothson (1972) suggests to me that some of the Dakota Sioux were also assuming parts and pieces of Oneota culture during the protohistoric period (Lothson 1972).

Traditional Oneota lifestyle (Henning 1970) varied depending upon the environment being exploited. Sites located west of the Mississippi River generally offer large quantities of bison bone, suggesting that the animals were killed nearby. Village size ranged from less than 1 ha to well over 243 ha; a few, such as the Utz village, a documented Missouri tribal location, appear to have been continuously occupied for several centuries. A few villages on the Mississippi River valley appear to have been fortified (Stevenson 1985). Some have earthen enclosed areas (Wood 1973), which may have functioned for defense, located nearby.

Pottery is the accepted diagnostic for Oneota cultural remains (Henning 1970). It is generally shell tempered. Globular jars with constricted orifices and rounded bottoms are the common form. Small bowls appear on some sites, but they are rare. Vessel size ranges from several centimeters in diameter to over 30 liters in capacity. Pottery characteristic of documented Ioway village sites is defined as "Allamakee Trailed" (Wedel 1959). Other diagnostics (Henning 1970) include simple triangular arrowpoints and small end scrapers. Groundstone tools characteristic of this culture include the large full-grooved maul, celts, grinding slabs, manos, and arrowshaft abraders. Bone and antler tools include bison scapula hoes, awls, needles, projectile points, and stone-processing tools. Antler, bone, shell and, on later sites, brass kettle parts and glass beads were used for ornamentation. The Ioway appear to have indulged in a lively trade of catlinite or pipestone from quarries in southwestern Minnesota and, perhaps, eastern South Dakota. Pipes, engraved tablets, and beads were made of this soft stone. In most Mississippi Valley Oneota sites, burial was usually restricted to cemetery areas, but human bone, sometimes cut, split, and burned, may be encountered anywhere. Some of the westernmost sites are characterized by circular burial mounds (Harvey 1979).

The traditional Chiwere Sioux homeland was located in southern Wisconsin. According to legend (Dorsey 1886), they were originally a single tribe, the first fissioning of which split the Winnebago from the others, then the Ioway-Oto from the Missouri, and finally, the Ioway from the Oto. Springer and Witkowski (1983) suggest that linguistically the Winnebago and Chiwere (Ioway, Oto, Missouri) had split by A.D. 1500. Judging from radiocarbon dates and archeological remains from the LaCrosse area, this date is correct. However, because cultural differences, particularly in ceramics, were well developed by that time, I believe that tribal fissioning had begun at least two centuries before 1500.

The LaCrosse area (Sasso et al. 1985) offers dozens of sites which form a laboratory for tracing regional Oneota cultural evolution dating from ca. 1300 to 1500 A.D. After 1500 A.D. no Oneota sites are found. The data suggest that the LaCrosse sequence reflects the evolution of the Orr Phase, the archeological 'culture' of the Ioway Indians.

It is pertinent to my discussion that no bison elements have been recovered from the LaCrosse area other than a few that were processed into tools. Bison bone elements are consistently found in Oneota refuse pits in sites on the west side of the Mississippi. It is my contention that people from the LaCrosse area were moving back and forth across the Mississippi River from at least 1200 A.D. They left the LaCrosse area permanently by 1500 A.D. and assumed residence on the lower Upper Iowa and Root River valleys. It was here that whites first contacted the Ioway Indians in the late 1600s (Mott 1938:238).

One of the attractions on the west side of the Mississippi River was probably the bison. Archeological evidence suggests that bison were readily available on the lower Upper Iowa and Root River valleys no later than 1500 A.D. and probably as much as two centuries before that time. Judging from paleoclimatic evidence (Wendland et al. 1987), steppe species, including bison, exhibited maximum frequencies during the Neo-Atlantic climatic episode (690-1100 A.D.), a time characterized by aridity. I suggest that late in this episode, small bison herds were established in the lower

Upper Iowa and Root River valleys and that these herds remained there through the succeeding Pacific episode (1150-1550 A.D.) and into the early Euro-American contact period.

Although the broad lower valleys of both rivers afforded excellent riverine collecting and suitable locations for gardening, the Ioway tended to be intermittent occupants of this locality. This pattern is quite apparent in the early historic record.

To the early white trader and explorer, the Ioway were an elusive tribe. Shortly after their discovery by Perrot in 1685, they vacated their villages near the Mississippi River, probably to locate on or near Spirit Lake (Wedel 1986:47). Wedel cites at least two reasons for this move; they were being harassed by the Mascoutens, an eastern, Algonkian-speaking group, and they wished to be near the Otos, probably for safety.

By 1700, when LeSueur sent his traders west from the Blue Earth River in southern Minnesota to find the Ioway, the Spirit Lake village was vacant. His men found (Wedel 1986:48) that the Ioway had joined the Omaha on the Big Sioux, probably where the Blood Run village site is located. Excavations there have yielded large quantities of bison bone, suggesting that the animals were readily available. Because of their gardening abilities, LeSueur enticed the Ioway to move back to a site near his fort (Wedel 1986:48), where they may have remained until 1702, when the fort was abandoned. They then may have returned to the Spirit Lake location, but did not remain there long

The Ioway lived in one or two villages in the Council Bluffs locale until about 1760 A.D., during which time they apparently acquired some horses (Wedel 1988:70-71). The site offered several advantages. The Ioway were suitably placed for trade with whites; were spatially insulated from their sometime enemies the Sioux, Sauk and Fox, and Osage; could maintain a favorable exchange with the Omaha, Oto, and Kansa; and could also hunt, fish, and garden. No Oneota site in the Council Bluffs locality has been excavated; the one known site was probably destroyed by flooding (Wedel 1988).

By the 1760s, the Ioway had moved to the Illinois side of the Mississippi River and occupied two villages (Mott 1938:251). In 1777, they were displaced by the Sauk and Fox and moved onto the lower Des Moines River valley where they settled on the Iowaville site (Mott 1938:275), near Selma. None of these sites has been professionally excavated. In 1821, the Sauk and Fox attacked Iowaville and killed many of the occupants (Pickard 1893). The Ioway moved west for the last time shortly after that encounter.

In contrast to several neighboring tribes, the Ioway were few in number; earliest reliable estimates suggest 1,000 'souls' of whom about 200 were warriors (Hodge 1910). They maintained peaceful relationships with tribes of similar size, the Oto, Missouri, Omaha, Kansa, and Ponca.

The Dakota Sioux, the Sauk and Fox, the Osage, and the Pawnee, all significantly larger tribal units and all with early access to Euro-American weapons and traps that made them technologically superior to the Ioway, were less peaceful. These tribes also became favored trading partners of the French, British, and Americans. Ioway relations with the Dakota Sioux, usually located immediately north of them, were occasionally antagonistic. The Ioway were often placed in an adversary position by the Sauk and Fox, who seemed to delight in pushing them out of their way. The Osage, located to the south and west, did them considerable damage on occasion as well. The Pawnee were rarely adversaries to the Ioway, but were a significant 'blocking presence' in their capacity to absorb the interest of white traders.

CONCLUSIONS

With its mixed subsistence base of bison hunting, fishing, gardening, and gathering of prairie peninsula resources, the Ioway cultural tradition was admirably adapted to the western prairie peninsula environment. However, their numbers relative to tribes which surrounded them, combined with the fact that Euro-American technological advantage reached them later than it did those neighbors, were prohibitive to their quickly gaining the power needed to compete either economically or militarily with their enemies. The well-adapted Ioway seemed to shift easily from dependance on one prairie resource to another. But, because of their low numbers and unfavorable geographical position, they were never afforded an opportunity to become as rich and powerful as some of their neighbors.

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TALLGRASS PRAIRIE SETTLEMENT: PRELUDE TO DEMISE OF THE TALLGRASS ECOSYSTEM

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Abstract. The tallgrass prairie was settled in less than a century and converted to cropland in the process. Rates of settlement and settlement patterns were influenced by natural features, origin of immigrants, presence of native Americans, available technology, and existing settlement patterns. The rates and patterns of settlement in Iowa are examined using local accounts, studies of specific factors, and early historical studies. The settlement and consequent demise of the Iowa prairie is a microcosm of what occurred throughout the tallgrass prairie ecosystem.

The tallgrass prairie is essentially gone. It is estimated that less than 3% of the 240 million acres of original tallgrass prairie remains. In Iowa, the loss was even more devastating; less than 0.1% of the original 30 million acres of prairie remains. Less well known is the rate at which the tallgrass prairie was converted to agricultural use. At the beginning of the nineteenth century, the tallgrass prairie was a major ecosystem occupying 240 million acres of mid-continent North America; by the end of the century, it was almost gone. In less than a century, Euro-American settlers obliterated a landscape that, according to Edwards (1948), was once thought to be so vast that it could not be subdued. It is astounding that an ecosystem of such magnitude could be vanquished so quickly. In fact, most of the tallgrass prairie was converted to agricultural use during the last 60 to 70 years of the nineteenth century. Rates of settlement and settlement patterns were influenced by features of the natural environment, such as vegetation type, topography, and rivers, and by the origins of the immigrants, the presence of native Americans, available technology, and existing settlement patterns. Table 1 summarizes the sequence and timing of settlement of the tallgrass prairie. Except for eastern outliers, overall settlement occurred between 1825 and 1920. The settlement of Iowa started in 1833 and ended with drainage of the wet prairie in 1920. The settlement and consequent demise of the Iowa prairie is a microcosm of what occurred throughout the entire tallgrass prairie ecosystem. This paper examines factors that affected the rates and patterns of settlement in Iowa. Information was obtained from personal accounts, local histories, and historical analyses of such factors as agricultural development, artificial drainage, land speculation, vegetation preferences of settlers, and geographic distribution of settlements.

Because the initial colonization of North America was on the eastern shore where woodland vegetation was dominant, the first two centuries of settlement occurred primarily in forests. Except for small patches that had been burned by Indians to raise corn, the farms of the eastern seaboard were carved out of a densely wooded landscape (Cochrane 1979). As pioneer farmers pushed westward across the Alleghenies during and after the American Revolution, they began to encounter *oak openings*, treeless meadows within the forest (Edwards 1948). Between 1790 and 1820, when the Pennyroyal section of Kentucky was occupied, they had a preview of the forthcoming prairie landscape. This grassland was designated *barrens* in reference to the near absence of forest cover. The vegetation of the uplands consisted of scattered clumps of trees, a dense undergrowth of shrubs, and occasional groves of large trees. For the most part, the valleys were heavily forested (Sauer 1963).

The early settlers of west-central Ohio found larger prairie openings in the forest; *islands of grassland* scattered across a dozen or more counties. These small prairies, dominated by big bluestem, Indian grass, and little bluestem, were outliers of the vast prairie farther west (Weaver 1954). As the wave of settlement moved westward from Ohio into Indiana and northwestward out of Kentucky and Tennessee into Illinois and Missouri, the prairie openings increased in frequency. For the most part, these openings were neglected, except as pasture for livestock.

Table 1. Approximate settlement dates for portions of the tallgrass prairie.

Tallgrass prairie area	*Approximate dates of settlement*
Barrens of Kentucky	1790-1820
Small prairie openings of Ohio	1815-1825
Northwestern Indiana portion of Grand Prairie	1825-1831
Oak openings and small prairies of southern Michigan, southern Wisconsin, Illinois, and northeastern Missouri	1825-1835
Well-drained prairie east of Mississippi plus eastern Iowa, northern Missouri, and southeastern Minnesota	1830-1850
Grand Prairie of Illinois	1830-1850+
Well-drained prairie west of Mississippi, except Oklahoma District	1850-1870
Oklahoma District	1888
Wet prairie west of Mississippi	1880-1920

Sometime in the 1830s, the westward movement confronted the true prairies of midcontinent North America. Although Edwards (1948) selected 1840 as the confrontation year, settlement maps based upon census data (Billington 1960) indicate an earlier time. Because the forests, the oak openings, and the small prairies of Michigan, Indiana, Wisconsin, Illinois, Missouri, and Iowa had been settled, prairie was the only remaining option available for the settlers. To people accustomed to woodland, the vast tallgrass prairie landscape must have been an awesome sight: "...the pioneers hesitated on the edge of the large prairies with their seemingly endless expanse of thick grass. There was a sense of vastness about them that seemed overpowering, an impression of greatness that could not be subdued" (Edwards 1948). But the prairies were settled. No bands played; no flags waved to mark the occasion; the conquest began out of necessity. Cautiously at first, using the earlier patterns of settling along the rivers and streams, at forest edges, in outlying groves, and along prairie margins, the occupation of the tallgrass prairie began. Consequently, the fringes of that vast 240 million acre prairie ecosystem were domesticated, but much remained undisturbed. Then, slowly, but persistently, the lines of settlement fanned out onto the prairie from the wooded river valleys. Although the settlers hesitated on the edge of the open prairie, and moved slowly at first; the pace of prairie settlement soon quickened. Once committed to settling on the prairie, they moved rapidly; the prairie frontier lasted only about 10 to 20 years in a particular area. In little more than ten years, the prime prairie land of the Grand Prairie of Illinois was settled. In Iowa in 1840, the western line of settlement encompassed less than a fourth of the state; by 1850, close to half of the state was occupied by settlers. The regions most distant from the watercourses were the last settled. Pioneer farmers reached the interior prairie of northeastern Illinois last among all regions of the state. In Iowa, settlement of interior counties lagged at least ten years behind those with major streams.

At the onset of the Civil War, the well-drained portions of the tallgrass prairie east of the Mississippi and in the eastern half of Iowa, northern Missouri, and parts of southern Minnesota were well settled. Post-Civil War expansion, from 1865 to 1890, completed the agricultural settlement of the tallgrass prairie to its western limits in eastern Kansas and Nebraska, southwestern Minnesota, and the eastern Dakotas (Edwards 1948, Billington 1960). The only unsettled tallgrass prairie was in the Oklahoma District; that remnant evaporated a few hours after a gunshot signaled the Oklahoma Land Rush of 1888.

The stage for Iowa's settlement was set in April 1832 with an ill-advised attempt by Chief Black Hawk and his Sauk tribe to return to their ancestral lands along the Rock River in Illinois. Prior to that attempt, the Iowa region was controlled by native Americans and was off-limits to all but a few Euro-American settlers. The defeat of the Sauk 15 months later at the Bad Axe Massacre expedited the *Black Hawk Purchase* so that on June 1, 1833, the first portion of Iowa was opened for settlement. The rush of people began at once; eager settlers jammed the trails and waited days to cross the Mississippi on ferries (Billington 1960). Initially, the settlement pattern was a natural expansion of the frontier from neighboring states. People from northeast Missouri and south-central Illinois overflowed into southeastern Iowa, and people from northern Illinois moved westward to Dubuque.

Available transportation strongly influenced the migration patterns of Iowa's early settlers. In the 1830s, there were two primary routes from the eastern United States into Iowa. Wagon travelers used the the *National Road*, which crossed the Allegheny Mountains from the Atlantic coast to the headwaters of the Ohio River. There, joined by settlers from above and below the Ohio, they continued on the National Road into Indiana and Illinois, heading toward the Mississippi River (Richman 1931). The ferries at Keokuk, Ft. Madison, and Burlington were the most frequent destinations. As an alternative, upon reaching the Ohio, they could proceed down river by flatboat and then find passage on a steamboat bound up river on the Mississippi. The second route involved water travel using canal boats and lake steamers through the Erie Canal and across the Great Lakes to Chicago. From Chicago, there were two choices: a wagon trail across Illinois entering Iowa via the ferry in the vicinity of Dubuque or a route following the Rock River, either by boat or by an Indian trail along its course, entering Iowa via the Buffalo ferry at the confluence of the Rock and Mississippi rivers just below Davenport (Harter and Stewart 1930). Prior to 1840, those entering Iowa by wagon outnumbered those entering by steamboat nine to one (Richman 1931). Later, as the number of people from the northeastern United States and foreign countries increased, the steamboats assumed a larger role.

Limited availability of ferries tended to concentrate the points of entry at Keokuk, Ft. Madison, Burlington, Buffalo, and Dubuque. Initial settlement was in the wooded eastern and southeastern parts of the state along the Mississippi River and its tributaries: the Des Moines, Skunk, Iowa, Cedar, Wapsipinicon, Maquoketa, and Turkey rivers. Early settlers tended to remain close to rivers and major streams. The watercourses provided ready transportation access into new areas, and as settlements were established, they served as routes to import and export commodities. The Des Moines, Iowa, and Cedar valleys were especially popular for home sites. By the late 1840s, settlers had followed the Missouri River north into the Council Bluffs area of southwestern Iowa (Swierenga 1968). According to Parker (1940), the tendency for settlement to ascend streams, a constant factor in settlement, is better illustrated in Iowa than any state except Ohio.

Although in some areas of the United States, native Americans impeded settlement, they had little effect on settlement in Iowa. Bogue (1963) conjectured that the *Spirit Lake Massacre* of 1857 may have slowed settlement slightly, but probably less than the depression of 1857. Billington (1960) suggested that the ruthless actions of the U.S. forces in the final battle of the Black Hawk War may have discouraged resistance and expedited treaty making for the removal of Indian tribes occupying the area. Usually, federal officials negotiated cession treaties in advance of the fast-moving frontier. As illustrated in Figure 1, the boundaries of the various cessions and the timing of the signing of the treaties affected where and when settlement could occur. The first treaty in Iowa, in 1924, was a minor land cession in the southeastern tip for the benefit of mixed-blood descendants of the Sauk and Fox. Following the Black Hawk Purchase of 1832, Indian titles were cleared from the remainder of the state by a series of treaties signed between 1832 and 1851.

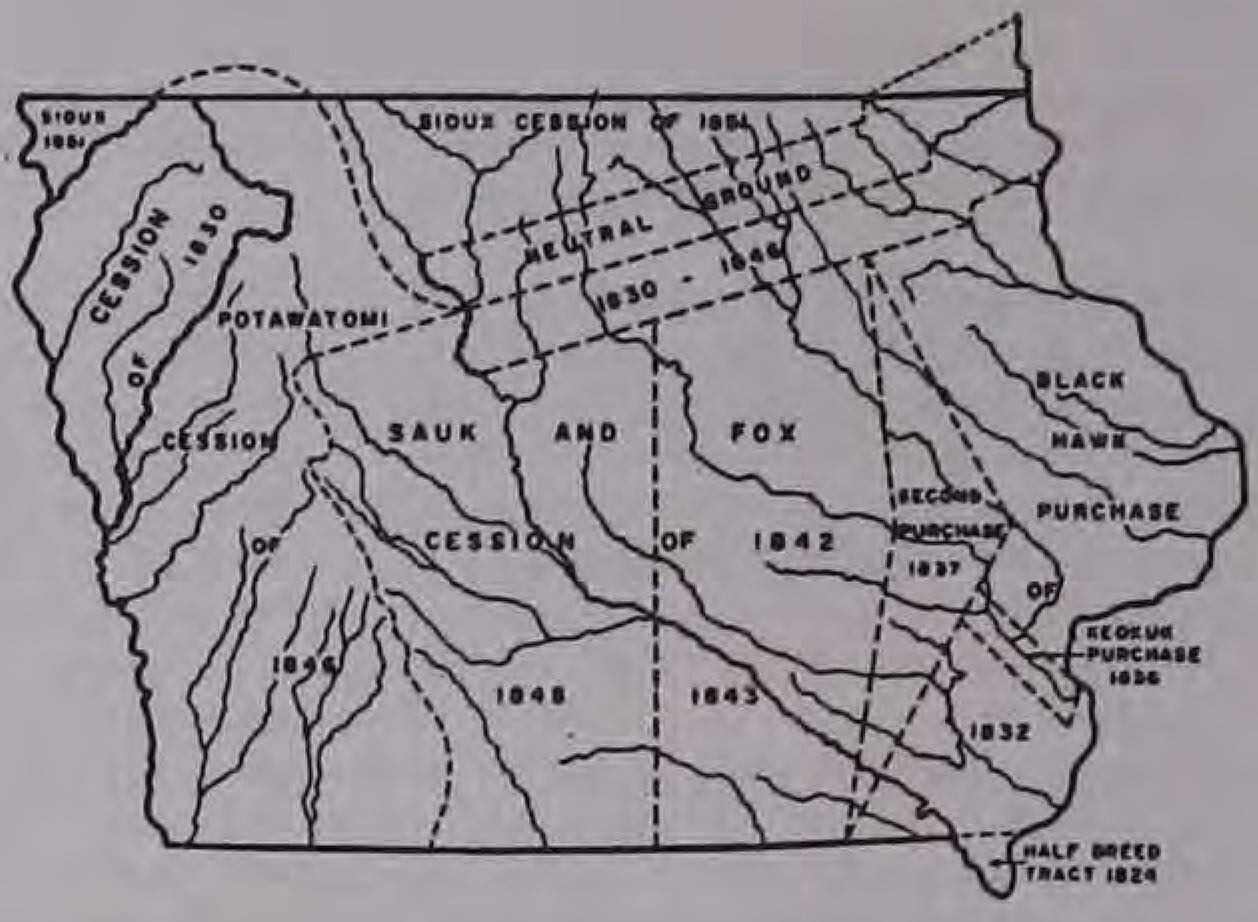

Figure 1. Indian land cessions by treaties of 1824, 1830, 1832, 1836, 1837, 1842, 1846, 1851 (adapted from Swierenga 1968).

Settlers were anxious to occupy the newly acquired land. In some cases, settlers would congregate along the boundary line prior to the opening of a new cession. Forty-five years before the famous Oklahoma Land Rush, the first North American land rush occurred when the eastern portion of the Sauk and Fox Cession of 1842 was opened at midnight April 30, 1843. At the deadline, troopers stationed along the border fired their guns into the air, and the settlers dashed pell-mell into the area to stake the claims they had scouted earlier. By sundown May 1, in Wapello County alone, more than one thousand farms were staked out, and a half dozen towns were laid out along the Des Moines River (Biggs 1865, Boyd 1867). It was reported that 10,000 people staked claims in the new purchase in the first two weeks (Gaylor 1843). The land to the east was not fully occupied, but the *sooners* were speculative, seeking the best water power and town sites and the choicest woodlands. The western half of the cession was opened midnight, October 11, 1845, and the scene of May 1 was repeated (Turrill 1857).

Goodwin (1919) wrote that the decade beginning in 1850 showed such an increase in Iowa population that a migrating tide swept over the state, inundating the valleys and hills with human energy. He cited several reasons for the population increase: completion of railroad lines to the Mississippi, the beginning of advertisement of western land by railroad companies, inducements from land companies and speculators, glowing accounts in emigrant guides, severe drought in the Ohio Valley, and a cholera epidemic in the Middle States. During the two years from 1854 to 1856, there was an increase in Iowa population of more than 190,000. Two quotes in Clark's article (1914) illustrate the magnitude of the influx. "The immigration to Iowa this season is immense, far exceeding the unprecedented immigration of last year, and only to be appreciated by one who travels through the country as we are doing, and finds the roads everywhere lined with movers." "The steam ferry at Rock Island was running 100 trips daily and couldn't handle all the traffic."

Population growth in Iowa slowed during the Civil War, but afterward, the annual increases were dramatic. These increases were primarily caused by four factors: discharged soldiers seeking new opportunities, an upswing in European immigration, the rapid development of farm machinery, and publicity surrounding the signing of the Homestead Act in 1860 (Harter and Stewart 1930). The expansion of settlement was accelerated by the rapid extension of railroad service. Prior to 1860, rail lines served only a portion of eastern Iowa. By 1870, three main lines extended across the state from east to west, and two others extended from the Mississippi River almost to the center of the state.

Census reports indicate that the rapid rate of settlement continued into the latter part of the century. During the 1870s, 430,595 people were added to the state. The population growth of Iowa from 1865 to 1900 was unprecedented, increasing from 756,209 to 2,231,853, a gain of almost 200%. Similar rates of settlement were occurring in the states adjoining Iowa (Harter and Stewart 1930).

According to the 1890 census, the population of Iowa was 1,911,896. Every county in the state had attained a density of 15 or more persons per square mile, the criteria for full agricultural settlement. Attaining this limit implies at least four families per section, one family per 160 acres (Harter and Stewart 1930). Figure 2 illustrates the regional and chronological development of Iowa from 1840 to 1890. The final stages of settlement in Iowa involved draining the wet prairie and coincided with the settlement of the remainder of the tallgrass prairie, with the exception of Oklahoma.

Patterns of settlement in the westward movement followed a general sequence from forest into grassland. A commonly held view is that settlers in the early and middle 1800s chose wooded areas along water courses and avoided prairies until they were forced by lack of forest areas to move onto the prairie. It is thought that earlier settlers avoided prairies, in part, because they believed the absence of trees indicated infertile soils. As late as 1860, population distribution in Story County, Iowa, showed a marked agreement with accessibility of timber (Hewes 1950). More significant reasons for selecting forested areas over prairies were probably the availability of wood for buildings, tools, and fuel and the accessibility of drinking water (Shimek 1911). Recently, some writers have challenged the view that forest sites were the first choice of settlers (Jordan 1964, Baldner 1984). They cite a number of examples in which the initial settlers selected sites on the edge of the prairie or on land that contained a significant portion of prairie. Jordan (1964) suggested that part of the problem stems from limiting the comparison of site selection to just forest or prairie and that a third choice should be included, an area of combined prairie and forest, or *savanna*. In a savanna, the settler could benefit from the advantages of both prairie and forest. The wood needed for construction and fuel was readily available, but the backbreaking work of forest clearing was avoided. As the line of settlement moved farther west, the availability of forest decreased, and the choices became more limited. However, wood remained an important commodity, and those that settled on the prairie often purchased wood lots as nearby as possible (Hewes 1950). The discovery of coal in some areas provided an alternative fuel and reduced the dependence on wood (Payne 1911).

As settlers became more familiar with the open prairies, there was an increased awareness of negative factors associated with prairie settlement. The menace of prairies fires and the ferocity of winter storms were significant factors. The modern technical term *wind chill* was unknown to the settlers, but they probably could have provided a good functional definition. In addition, the tough, heavy, prairie sod, formed from intertwined roots of the prairie plants, was too much for their inadequate implements and limited numbers of draft animals. Much of the flat prairie was low, marshy, and poorly drained; many settlers suffered from fever and ague (malaria) on these wet prairies. Access to streams for water transportation was limited, and in the spring, mud caused the prairie trails to be practically impassable to horses and wagons (Sauer 1916, Weaver 1954).

Berry (1927) was of the opinion that artificial drainage was as important as the railroad in bringing new prairie land into agricultural use. Although artificial drainage converted thousands of acres

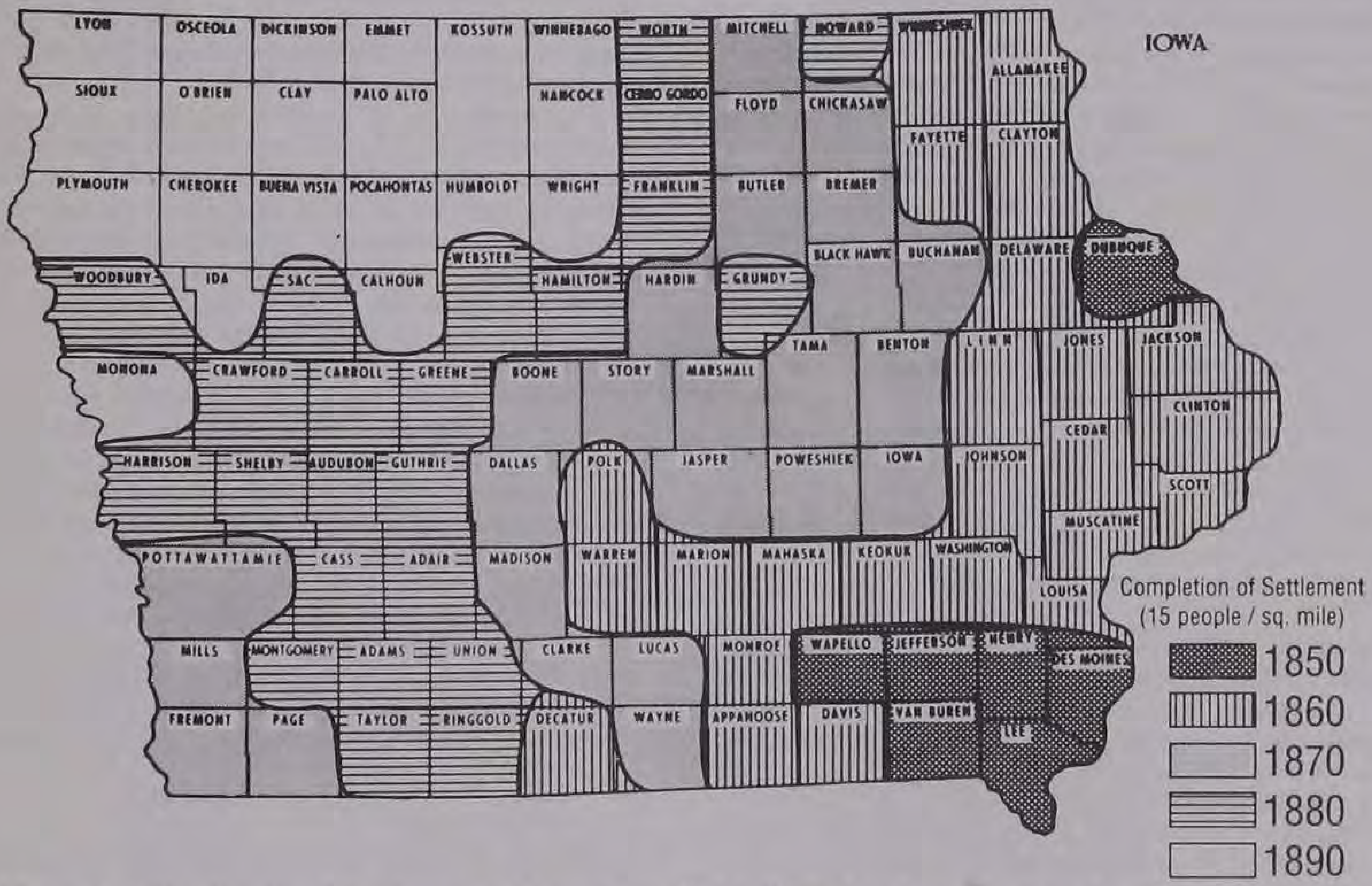

Figure 2. Chronological and regional development of Iowa from 1840 to 1890. Land was considered *settled* when a density of 15 or more people per square mile was attained (adapted from Harter and Stewart 1930).

of prairie into some of the world's richest farmland, Berry, perceptively, raised the question of whether Iowa, in particular, and the United States as a whole, really benefited from the drainage. In his opinion, the increased corn production resulting from drainage could have been accomplished on corn lands already in use. He noted that, with the exception of a few years during World War I, drainage contributed to surpluses that upset farming conditions to the point of threatening the foundations of agriculture. He further indicated that artificial drainage lowered ground water throughout Iowa and destroyed most of the valuable breeding ground of migratory birds in the central United States.

The fertility of prairie soil undoubtedly contributed to the prairie's demise. The extent of the original prairie and the distribution of rich, black soil correlate well. A study directed by Marbut (1934) classified approximately 26 million acres of Iowa as Grade 1 agricultural land. Grade 1 correlates well in amount and distribution with the black, fertile, prairie soils. The black color indicates a high content of organic materials, accumulated over time from a residue of prairie vegetation with extensive root systems. It is ironic that the prairie was initially thought to be sterile because it did not support trees. Atwater (1829), a long-term proponent of prairie fertility, disagreed with that opinion of the Iowa prairies: "We are often told by eastern scientific empirics who have seen them of the sterility of the soil where the prairies are, but the very reverse is the fact." Albert Lea (1836) was impressed by the agricultural productivity of the prairie soil. Undoubtedly, by the early 1840s as farmers began to bring the prairie under cultivation (Bogue 1963), many were becoming aware of the fertility of the prairie soil.

The plow is symbolic of the demise of Iowa prairie. The tough prairie sod was an almost insurmountable obstacle to the early prairie settlers. The extensive intertwined root systems of the prairie plants did not yield to the plows developed for turning forest soils (Bogue 1963). Much of the initial prairie breaking was done with massive unwieldy breaking plows pulled by several yokes of oxen and operated by custom crews (Coffin 1902). Subsequent technological developments changed the problems of plowing prairie sod from formidable obstacles to temporary inconveniences. In 1837, John Deere designed a one-piece, wrought-iron plow with a cutting edge of steel on the share. Within 20 years, his plant in Moline, Illinois, was producing 10,000 plows a year (Cochrane 1979). Low cost plow production was accomplished in the 1860s when James Oliver perfected the process of making chilled cast-iron plowshares (Bogue 1963). These plows proved to be very effective for breaking prairie. Madsen (1972) compared the utilitarian beauty of the Deere plow with that of the Lancaster rifle. In terms of accelerating the destruction of the prairie, it might better be compared with the Henry or Winchester repeating rifle or, perhaps, the Gatling gun. Technological improvements in farm machinery from the 1840s to the 1870s reduced labor, eased farming drudgery, and accelerated the conversion of prairie to cropland. Successful models of harrows, planters, cultivators, reapers, and threshers came into common usage in the tallgrass prairie region during the 1860s and 1870s. By the mid-1870s, Deere and Company and the Oliver firm were each marketing a *sulky plow*, one or two plows mounted on a wheeled frame with a seat, which enabled farmers to plow land more rapidly while sitting down (Bogue 1963, Cochrane 1979).

By trial and error, the settlers determined the most effective way of converting prairie to cropland. They had to turn the sod late enough in the season to prevent regrowth but early enough to allow time for rotting before autumn (Bogue 1963). In the 1870s, they learned that a crop of flax sown on April-plowed ground could withstand the competition of the native plants and apparently helped rot the sod (Coffin 1902). Not only did the settlers till the land and plant crops, but their disturbance of the ground allowed numerous alien species to move in and compete favorably. Bluegrass could endure the plow and became quite common; plantain came with the settlers; dandelions followed shortly thereafter. However, as late as 1854, there were no dandelions in some of the eastern counties, and, surely, none to the west. In that year, some settlers sent to Pennsylvania for dandelion seed (MacBride 1895). Cockleburs thrived on land disturbed by cultivation, as did the ragweeds, which spread beyond their former natural confinement.

The wet prairie was one of the last frontiers of the tallgrass prairie. In converting the tallgrass prairie to cropland, the well-drained prairie ridges were the first to be plowed. The farmer who settled on land with wet prairie broke the high ground and looked to lowlands and sloughs for pasture and wild hay. Much of north-central Iowa, southwestern Minnesota, and the Grand Prairie of Illinois was topographically controlled by the Wisconsin glaciation. Because surface drainage patterns were poorly developed, large areas were frequently water covered or wet much of the year. Wet prairie beyond the Wisconsin drift boundaries was caused by relatively impervious subsoils and local drainage limitations. These extensive stretches of wet prairie delayed settlement in Iowa and in Minnesota and Illinois. Great stretches of Iowa's wet prairie lay in virgin sod while settlers by-passed it to gamble five years of their lives trying to win a free homestead in the sandhills of Nebraska. Drainage of the wet prairie was a long-term effort; drainage attempts prior to 1870 were limited (Bogue 1963). Drainage on a large scale did not begin in Iowa until about 1888 (Berry 1927). Each year thereafter, an increasingly larger acreage of wet prairie was brought into cultivation.

Based upon population density, Harter and Stewart (1930) concluded that agricultural settlement of Iowa was completed by 1890; whereas Bogue (1963) selects 1900, when most Iowa counties recorded their largest total of farm units. By the turn of the century, most of the Iowa prairie had been converted to farmland; the prairie ecosystem was close to extinction. Even the prairie slough, usually the last to go under the plow, was lamented as becoming obsolete (Aldrich 1903). In 1911, Shimek (1911) noted that native prairie was fast disappearing and being replaced with artificial groves, cultivated crops, and introduced weeds. Practically all the wet prairie had been drained for cultivation by 1918 or 1920 (Berry 1927). By 1925, comparatively little native prairie remained in Iowa; a few unbroken tracts were scattered about the state, especially in the northwestern quarter, but even these were disturbed by pasturing and mowing (Shimek 1925).

John Madsen (1972) captures the essence of the demise of the prairie ecosystem: "We spent our tallgrass prairie with a prodigal hand, and it probably had to be that way, for these are the richest farm soils in the world... tallgrass prairie is the most difficult of all native America to conserve... because it is the worlds's most valuable farm soil." It is unbelievable that so vast an ecosystem could be eliminated in so little time. Two hundred and forty million acres of tallgrass prairie were converted to agricultural land in about seventy years.

Apparently the nineteenth century settlers were not aware that an entire ecosystem was being obliterated. Perhaps there was just too much; abundance tends to create an illusion of limitlessness. As is so often the case, a heritage was lost before its value was tallied or its passing noted. The pioneering characteristics that prompted people to leave a sheltered society to settle a new land were instrumental in the demise of the tallgrass prairie. Motivated by a need for personal accomplishment, burdened with a daily struggle against an overwhelming prairie wilderness that could destroy much of their fragile gains, and ultimately justified by a perceived destiny to feed the world, the prairie settlers plowed and planted the tallgrass prairie ecosystem into extinction (Smith 1981).

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THE PRAIRIE AS PERENNIAL SYMBOL

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Abstract. For much of its cultural history, the prairie has served as a dual symbol of midwestern life. Drawing on two conflicting but interdependent traditions, elements of which can be traced back to the earliest explorers and promoters, artists and writers have in effect carried on a debate about the meaning of the region's culture. In one set of attitudes, represented by Cather, F. L. Wright, Jensen, Curry, and Wood, the prairie land is celebrated as the heartland of American democratic vitality and productivity. In the other set of attitudes, expressed by certain early explorers as well as writers Garland and Lewis, prairie life is attacked as barren and boring, a cultural desert. Recently, new cultural meanings seem to be forming around the idea of the prairie. It is being seen as a symbol of renewal and sustainability and as a reminder of our past mistakes in conservation. In typical midwestern fashion, this new symbolic meaning of the prairie is a middle ground with regard to land use, representing a bridge between the extreme positions of non-use and exploitation.

Printed in the program for this conference is a quotation from Aldo Leopold: "What a thousand acres of Silphiums looked like when they tickled the bellies of the buffalo is a question never again to be answered and perhaps not even asked." It is a sentence which combines an overwhelming sense of loss with the barest glimmer of hope—hope that someday we might be interested enough in our prairie heritage to inquire about it. Leopold's particular image here is a figure for the larger issue of whether America's most distinctive ecosystem will ever become an intimate part of our cultural consciousness, that is, part of a "refined taste in natural objects," in a way that combines knowledge, beauty, love, and stewardship.

My argument here is that it might, that the glimmer I see in Leopold's qualified negative is a brighter glimmer, though still a glimmer, than it has been for years.

I find my reasons in history, in connecting past attitudes toward the prairie with a variety of present ones in a way that suggests the prairie is once again becoming a vital symbolic focal point for the Midwest. That is, around the idea of the prairie, a wide range of creative activities and values have been coalescing in recent years, a consciousness of the prairie that expresses itself in many ways: in new novels, poems, paintings, and photographs which make significant use of the prairie idea; in books of prairie natural history; in essays on prairie life and its meaning; in prairie restorations both public and private; in the revival of interest in older prairie writers and painters by critics, scholars, and publishers; in prairie gardens; in the renewed call for a national prairie park; and in scientific concern for the prairie from Wes Jackson to conferences such as this. It seems likely to me that something is in the air that is not simply of passing note but that is part of a longer tradition of thought, a set of values which are connected to our sense of midwestern life and, perhaps, in a related and parallel way for prairie-dwelling Canadians to a sense of their regional identity also (Fairbanks 1986, Ricon 1973, Thacker 1989).

This is one reason I speak about the prairie as perennial symbol. It is a symbol which has recurred continually in the cultural images of the Midwest, cropping up again and again in important ways. These past prairie images give historical perspective to any reading of the recent prairie interest of the last two dozen years. In a number of ways, the prairie defined what the Midwest was and what it stood for. It was the heart of the heart of America, the *land* in heartland.

There were two views of the prairie from the earliest explorers and travellers through the boosters and settlers to the artists and writers who interpreted and defined it. One image was of the prairie as an enormous fertile and fecund space, a place of great potential for economic wealth, an area in which American democratic aspirations could truly be realized, a land open to possibilities for everyone. In the vast prairie space, organized by the National Grid and open to all hard workers through the Homestead Act, the Jeffersonian dream of a society of comfortable agrarian civility could at last be realized, according to this attitude. From William Cullen Bryant on—Bryant was the first major American writer to actually see the prairie and render it in imaginative literature—the prairie was a desert that could be made to bloom as soon as it was improved, that is, as soon as religion, agriculture, and families occupied it. Native Americans did not count in the imaginations of most Americans; they were either absent from this image or a temporary impediment to turning the prairie into America's breadbasket. Even Willa Cather, the greatest and most sympathetic writer of prairie life, left the Native Americans out of her prairie land. When, in *O Pioneers*!, Alexandra realizes her love for and commitment to the prairie, Cather (1913) writes: "For the first time, perhaps, since that land emerged from the waters of geologic ages, a human face was set toward it with love and yearning."

Not all who saw the prairie or who lived on it were enthusiastic, of course. A second, contrary view was that the prairie was a sterile, barren, Godforsaken place, boring, monotonous, violent, and closed off from possibilities. It was a desert, not because of a lack of water but because it was beyond redemption, fit only for marginal peoples, red and white, a savage land of violent weather, violent geography, and violent creatures. Those who did venture out onto the prairie had in store for them more terrifying encounters than those with warriors and outlaws, however. They might encounter no one at all and, so, have to face the vastness and scale of the prairie alone. In a word, they might become lost. The danger, said George Kendall in 1845, (Kendall in Conron 1974), was not so much to physical safety as to mental stability. "*To be lost*," he said, "has a complex and fearful meaning.... All is lost, except a maniacal impulse to despair, that is peculiar and indescribable." The prairie could be a place of crushing loneliness, and this secondary, dark theme plays off against the dominant sense of optimism from the beginning of European encounters with the prairie (Thacker 1989); it becomes especially prominent with the rise of realism in American literature in the last third of the 19th century, pervading the stories of pioneers and farm families such as those of Hamlin Garland; and it received its most famous expression in the character of Beret in Ole Rolvaag's *Giants in the Earth* in 1927. Finally, the "terrible space" of the prairie land has been noted as recently as 1985 in Paul Gruchow's collection of essays, *Journal of a Prairie Year* (Gruchow 1985): "Newcomers to the prairie are at first disconcerted by its nakedness. Later they wish it weren't so private." Gruchow catches the essence of the problem the prairie creates for the imagination: What sort of reaction can one have to a land that both dwarfs one with its scale and at the same time concentrates the psyche on the only point of reference, the self?

There is, then, plenty of darkness in our heritage of prairie images which is not hard to find if you look for it. The land is linked to suicides and madness, to defeat and conformity and spiritual deadness: "Our minds grow heavy," says Willa Cather's Alexandra, a criticism all the more telling in that it comes from one who loves and celebrates the prairie land (Cather 1913). Nevertheless, the dominant image has been a sunny one, and the meaning we gave to the prairie is of a place in which the great act was settling the land in a democratic gesture. The land would return abundance for our efforts, cooperating in its own submission with a "deep sigh of happiness" (Cather 1913). In the American imagination, winning the West was an act of high adventure, but settling the Midwest was a domestic drama of family, work, produce, and stability. These rhythms of everyday life, common sense, comfortable livelihood, and civility were a middle way between the extremes of eastern urbanization, on the one hand, and western freedom and individualism, on the other hand.

Our pride in turning the prairie into the American breadbasket often led to smugness, and a number of our writers have been quick to point this out, most notably Sinclair Lewis in *Main Street* (1920). The potential for human dignity and democratic heroism, which Whitman saw as the promise of the American prairie character in the 1870's, seemed a failed promise to Lewis 50 years later, one badly in need of debunking. For Whitman, it was the prairie that gave us the most important Americans of the day, Lincoln and Grant "— vast-spread, average men—their foregrounds of character altogether practical and real, yet (to those who have the eyes to see) with finest backgrounds of the ideal, towering as high as any" (Whitman in Conron 1974). But for Lewis, all that remained in the 20th century was Carol Kennicott, "a rebellious girl [who] is the spirit of that bewildered empire called the American Middlewest." And Carol is defeated by the small minded materialism of the town (Lewis 1920). Recently, and despite its nostalgia, Garrison Keiller's *Lake Woebegone Days* (1985) gives more than a passing nod to this critique, most explicitly in the 95 theses with which he indicts the prairie town.

But the vital potential of the idea of the prairie has been demonstrated repeatedly in 20th century culture. In the years before WW I, it is seen as the inspiration for the innovative domestic architecture of Frank Lloyd Wright and the Prairie School which followed his lead. The prairie influence was not only a matter of the exterior style for Wright, where the long horizontal lines of the prairie house's roof and other elements deliberately reflected the landscape, but it was felt in the interior arrangement of space as well. Wright broke open the box-like rooms of the Victorian family home to express what he saw as prairie values: he made an open space of the living room and dining room, one which flowed from and centered around the family hearth; he opened the exterior walls with banks of windows to connect the interior of the house with natural light and vista; and he sited these homes in ways that emphasized privacy and kept neighbors at a friendly distance. These were homes, said Wright, for "the Western citizen of the great prairies. The real American Spirit, capable of judging an issue for itself upon its own merits, lies in the West and Middle West where breadth of view, independent thought, and a tendency to talk common sense into the realm of art as in life, is more characteristic" (Wright in Kaufman and Raeburn 1960).

Contemporary with Wright is the work of Jens Jensen, the great midwestern landscape architect, whose urban parks, memorial gardens, and private landscapes took the prairie space as a central design element. Grass meadows, prairie rivers, and local plants and trees were the fundamental design materials. Jensen combined these elements according to an aesthetic philosophy that championed the indigenous beauty of the Midwest as the most essentially democratic and American. A symbolic prairie, a meadow opening in the trees and shrubbery using wild flowers but not wild grasses, was central both to the design and the philosophy of Jensen's work. Prairies, though vast, were hospitable, friendly, and reassuring in their effect on people: "They are the Mid-American empire, the heart and moving force of our great country" (Jensen 1939).

This sense of the prairie land as central to midwestern identity, and so to a larger American identity, reappears in the 1930s in the Regionalist movement in American painting, most notably in the work of John Steuart Curry and of Grant Wood. We are invited to see the meaning of the land as essential to understanding those who live on it and work it as an elemental dramatic struggle in Curry's paintings and with a whimsy that overlies the elemental stability of the earth in Grant Wood's work. In both artists, though in different ways, the prairie land is linked to a pride in local people and their ways and to a democratic appreciation of the common man, of home, and of the dignity and satisfaction of everyday rural life (Czestochowski 1981).

Like Wright and Jensen, Curry and Wood represent the continuity of the prairie as an important cultural image in the first half of the 20th century. Taken together, all four artists found the prairie land to be an inspiration to their creative work and a symbol of what was best and most typical in America. But they also represent the development of a new emphasis within that image. It would seem that as the actuality of the prairie disappeared under plow, road, and city block, the prairie as an idea took on the added possibility of a new, more harmonious connection with the earth. As we destroyed the wild prairie, our writers and artists were paradoxically inspired by the prairie idea in ways that laid the basis for a changed consciousness of how to live with the land.

The prairie, then, is a perennial symbol in its recurrence. But it has become perennial in another, second sense as well. Not only does it manifest itself regularly in our history as an emblem of fundamental values in midwestern life, but in its latest flowering it is specifically about renewal, regeneration, restoration, and linking the past to the present. It is about ecological sanity.

Earlier I cited a number of examples that I felt might represent a coalescence of attitudes around this idea of the prairie as renewal. In order to characterize a bit more fully what I mean, I want to describe briefly two current examples of the new meanings which the prairie idea seems to embody. The first is from the work of Wes Jackson, specifically the key concept in his book *Altars of Unhewn Stone*. Jackson argues that we need to create a new "domestic prairie" through developing perennial grain crops for livestock and human food to replace annual plowing and planting which wastes the soil. The continuity of this concept with antecedent images of the prairie and the Midwest is evident but so too is a passionate need for us to learn from our failures and abuses of the land. His chapter, "Living Nets on the New Prairie Sea," combines both old and new ideas of the prairie. Here we have a concept which values agricultural production and the prairie land as food giver. It is, recognizably, the continuing notion of the prairie as breadbasket. Science and technology are to be employed to satisfy human needs—but in a radically new way. Jackson wants to change the standard by which we measure success on the prairie. Short term exploitation must give way to a vision of sustainable land use. In effect, the domestic prairie represents a middle ground between monoculture farming and the kaleidoscopic diversity of the wild prairie. It embraces science but measures science against the standard of wildness. Also, it is a metaphor for frugality. In short, the domestic prairie is the midwestern answer to the global dilemma of how to establish a new relation to nature and the land while still maintaining our civilization (Jackson 1987).

A second example may be less familiar but is no less instructive. In April, 1988, 18 months before *The Atlantic Monthly* was to publish a profile on Wes Jackson and his ideas, unfortunately entitled "Back to Eden," (Eisenberg 1989), *Harper's* published an essay by Frederick Turner (1988) called "A Field Guide to the Synthetic Landscape." Turner's essay is a complement to Jackson's—the poet's view coincides with the scientist's. Turner is in his own way also trying to close the gap between wilderness and agriculture, between past and future attitudes toward the land. Here the approach of the poet/essayist attempts to establish a new poetics of ecology rather than a new agronomy. Turner argues for ecological restorations as a guiding metaphor for an environmental ethic and his major example is . . . restoring prairies. Turner sees in the act of prairie restoration a complex of meanings that are premised on cooperation, mild change, and human participation in the natural processes of the world. Fire is, for Turner, the great discovery of prairie restoration. It signifies patience and humility, working with nature, and redemption: we are needed to repair what we have spoiled. "Perhaps one day prairie burning will be one of the great ritual occasions of the Midwest— a sort of festival of Dionysus, the god of inexhaustible life—an occasion for drama, music, poetry, and storytelling" (Turner 1988).

While surely the most bardic and prophetic image of the prairie since Whitman, Turner's vision is one which catches at the extreme the renewed interest in prairie as a figure for an ecological consciousness that includes human use of land in a more harmonious way. It may stretch one's view of the Midwest to see us all dancing around in prairie bacchanals, getting naked on the prairie as it were, but to Turner, as to Jackson, as to many in the last two decades who are drawing on the prairie for inspiration or out of delight or from an ecological concern, the prairie exemplifies a creative middle way. It avoids the amoral view of the land as simply an exploitable commodity governed only by the cash nexus, on the one hand, and the self-righteous and nearly misanthropic rejection of 20th century culture, on the other hand. The perennial prairie idea is, I think, about how to live with the land, to save what remains, to recreate what we can, to honor the past, and to pattern our future.

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THE ROLE OF FAMILIARITY IN PRAIRIE LANDSCAPE AESTHETICS

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Abstract. The study reported here focused on the prairie—a type of landscape that seems to be differentially appreciated by people in general and which fails to achieve high ranking given the assessment approaches currently in use. In particular, the study examined the relationship between the level of familiarity one has with the prairie and the level of appreciation one feels for it. Familiarity was divided into four aspects: Knowledge, Experience, Background, and Predisposition. Nearly 400 participants were measured for their levels of these aspects and for their preferences of 41 prairie scenes. The four familiarity aspects proved to be influential in the preference ratings in the majority of cases. Thus, it is clear from this work that familiarity with prairie landscapes affected the preference of those landscapes. It appears that those who find beauty in these landscapes possess knowledge or experience others do not share.

INTRODUCTION

To some people tallgrass prairie represents a rare and fascinating landscape—complex, subtle, and incredibly beautiful. Yet many people find little interest or visual pleasure in these grassy plains. In fact, this type of landscape would fail to achieve high rankings given the visual assessment approaches currently in use (Grden 1979). It is this difference in landscape appreciation that inspired this study and spurred the following questions: Why do we find more beauty in one landscape than in another? Why do some prefer mountains while others prefer forests, savannas, or prairies? Could it be that the landscapes we find most aesthetically pleasing are those we are most familiar with?

In trying to answer these questions, one is drawn to an examination of the relationship between familiarity and preference. There seem to be different categories of landscapes when considering this relationship. There are landscapes that will be highly preferred or not preferred regardless of the experience or knowledge one may have of them. There are also landscapes that may be preferred much more or less by a person who is knowledgeable about and experienced with (familiar) those landscapes than by a person who is not. The landscapes of the prairie, and perhaps of other open lands such as tundra and desert, appear to fit this second category. Thus, this work sought to study the relationship between familiarity with tallgrass prairie landscapes and preference for those landscapes.

That environmental familiarity should affect perception and possibly aesthetic appreciation of a landscape is not a new concept. This idea was expressed by Aldo Leopold in what Callicott (1983) calls Leopold's land aesthetic. The basic tenet of the land aesthetic is that as one develops "biological literacy," one is able to recognize the beauty of overlooked natural environments or those common landscapes close to home. Leopold felt that as our environmental understanding of a landscape increases, our perception of that landscape changes, a change that can increase our aesthetic harvest from that landscape.

The major question examined in this work was drawn from Leopold's concept: Is there a discernible relationship between environmental familiarity of prairie landscapes and aesthetic reaction or preference for those landscapes? Environmental familiarity was viewed as having several interrelated aspects—knowledge, experience, background, predisposition.

Knowledge

As used here, Knowledge refers to information one might gain from indirect landscape study, such as from books, lectures, articles, classes, landscape painting, or photography, which deal with prairie landscapes. The information may deal with biophysical components and/or cultural components of these landscapes. The main distinction here is that knowledge comes from sources other than the landscape itself, namely, the writings, words, or interpretations of others.

Experience

Experience refers to information gained from direct landscape study. One might gain this type of information from exploration of prairie landscapes on foot or from a vehicle. The type of information gained would depend upon the individual, but it would be the result of a direct correspondence between observer and landscape.

Background

This aspect of familiarity includes such issues as where one has resided. If a person were born and raised in a prairie landscape, one would assume that person would have a better understanding of prairies than would a person born and raised in a forest environment.

Predisposition

This aspect of familiarity refers to one's inclination or bias towards a particular environment. Predisposition may be related to knowledge, experience, and background. For instance, if one is inclined to favor forest environments, it is reasonable to expect knowledge and experience of these landscapes to be greater than for landscapes one is less inclined towards.

These aspects of familiarity are highly interrelated. Each of these sources was measured in this study with the belief that working together they form the foundation of environmental familiarity of prairie landscapes.

Preference

Preference quite simply is the level of appreciation one feels for a given landscape—how much one likes a landscape. This may sound trivial, but preferences are important in our ability to function. Kaplan and Kaplan (1982) feel preference "can be viewed as an expression of the evaluation of one's possibilities. It is an extension of the perceptual process; like prediction, it enhances one's readiness to act even though no action may be called for at that particular moment."

To summarize, this work is about prairie preference and the role of knowledge, experience, background, and predisposition in coloring this preference. The following section presents the methods used in a pair of studies which explored various aspects of familiarity.

METHODS

There were two separate studies in this work. Both studies assessed familiarity through self-reported measures of: Experience, Background, and Predisposition. Knowledge, an additional aspect of familiarity was assessed in the first study (Study I) and manipulated in Study II. The manipulation involved a lecture focusing either on the ecological or the cultural/historical aspects of prairies; a control group received no instruction.

Study I

There were 197 participants in Study I. All participants were students at Kansas State University. Three instruments were employed in this study: the familiarity questionnaire, the Environmental Preference Questionnaire (EPQ), and the preference rating of 41 prairie landscape scenes. All instruments used in this work can be found in Keane (1990).

Familiarity questionnaire.

This was a brief questionnaire containing items intended to measure the participant's background, experience, and knowledge of prairie landscapes.

Environmental Preference Questionnaire (EPQ).

This instrument was employed to measure the participant's predisposition for a range of settings. The EPQ is a 70 item questionnaire devised by Stephen and Rachel Kaplan at the University of Michigan in 1970. The purpose of the EPQ "was to identify sources of satisfaction and patterns of preference pertaining to environmental settings. The focus was not so much on past experience as on current outlook" (Kaplan 1977). For this study, a slightly revised version of the EPQ was used. This revision entailed dropping some items from the Kaplans' EPQ and replacing them with items dealing with grassland and savanna settings.

Preference rating of 41 prairie landscape scenes.

The 41 scenes (selected from a pool of approximately 300) used in this work were selected to portray prairie landscapes in a typical rather than a dramatic fashion. All landscapes portrayed can be found within 20 miles of Manhattan, Kansas. Participants were asked to view 35 mm color transparencies (slides) depicting prairie landscape scenes and to record their level of preference for each scene. The preference responses were given on a five-point scale where one equalled very low preference, and five equalled very high preference.

Study II

While Study II included a similar set of familiarity and preference measures, it differed substantially from Study I in its effort to provide educational information about prairies. There were 204 participants in Study II. Again, these participants were Kansas State University students, but they were a completely different group of students than employed in Study I.

Educational treatments.

Educational treatments were administered as a way to enhance Knowledge about prairies. Treatments were administered to the participants in the form of one-hour lectures supplemented with color slides. One treatment dealt with *ecological factors* of prairie landscapes. Topics discussed in this treatment included origins of prairie; prairie landforms, soils, vegetation, and animals; prairie climate; and the importance of fire. A second treatment dealt with *cultural and historical factors* of prairie landscapes. Areas covered in this treatment included landscape evolution or natural history; human use history, beginning with European discovery of the prairies by the Spanish; and prairie literature—the writings of those who experienced the prairie in the past and in recent times. A third treatment was a control group in which no lecture or information of any kind was received by participants.

Three instruments were used in Study II: a familiarity questionnaire, the EPQ, and the prairie landscape slide preference rating. The EPQ and the preference rating were the same as discussed for Study I.

The familiarity questionnaire, used to measure knowledge, experience, and background, differed in some respects from the Study I version. Study II employed a greater number of knowledge items with a wider content range than Study I.

Testing of participants.

Administration of the familiarity questionnaire, EPQ, and the rating of prairie slides occurred during the first 20 minutes of the lab sessions that students in the course supplying participants attended. There were nine different sections with 15-25 students each. The testing of participants occurred over a two-week period following the lectures, with each participant being tested once.

The staggering of test times was intentional. If the treatments were successful in increasing landscape knowledge, it was felt that this increase would likely be short-lived; thus, if knowledge was affected by the treatments, there should be a decrease in knowledge scores over the course of the testing period.

Landscape and Predisposition Categories

Because of the large number of items in the preference rating (41 slides) and the EPQ (70 items), both were subjected to Category Identifying Methodology (CIM) (Kaplan and Kaplan 1989). The CIM used involved two different analyses. The primary technique was Smallest Space Analysis III, a non-metric factor analysis procedure developed by Lingoes (1972). The second technique was a hierarchical cluster analysis procedure called ICLUST (Kulik et al. 1970). This methodology uses the participant ratings to produce categories of scenes or questionnaire items that are similarly perceived or experienced. These analyses produced five Landscape Categories (from the 41 slides) and six Predisposition Categories (from the 70 EPQ items). I then examined these categories and named each for the dominant characteristic or theme common to the category. The Landscape Categories are listed and briefly discussed below; the Predisposition Categories will be addressed in the discussion of results.

RESULTS

CIM produced the following five Landscape Categories:

Distant hills.

Scenes in this category had flat-topped hills in the background and some detail in the foreground provided by shrubs or flowering forbs. Visually, the scenes have a sense of depth and vastness.

Foreground grass.

The landform in the scenes of this category is gently rolling and all scenes are dominated by grasses from foreground to background. Again, these scenes appear vast, and one feels that nothing is hidden from view.

Warm-hued color.

Color is the common characteristic of this category, particularly various shades of brown, red, yellow, and orange. This category also shows more diversity in vegetation and landform than the previous categories.

Foreground texture.

The scenes here have a rough texture in the foreground that appears to impede movement into or through the scenes. These scenes also show a greater occurrence of woody vegetation than do the scenes in the previous categories.

Wooded draws.

The common characteristic of wooded draws is landscape pattern, in particular, the pattern created by streams. There appears to be a balance and order to the woody and grass vegetation.

The mean preference scores for the Landscape Categories had the same pattern for both Study I and Study II. This order of preference is the same order in which they were presented above, with Distant Hills being the least preferred and Wooded Draws the most preferred in both studies.

Familiarity Variables

Analysis of the familiarity questionnaires led to the following breakdown of the familiarity variables.

Background.

Background was divided into two categories, participants from rural background and those from non-rural background.

Experience.

The experience measure was divided into three levels (Low, Medium, and High) based on the overall distribution of the sample.

Knowledge.

This measure was also divided into three levels (Low, Medium, and High) based on sample distribution.

DISCUSSION

Study I

The relationship between the familiarity variables and preference for the Landscape Categories for Study I is shown in Table 1. As Table 1 shows, Study I participants from rural backgrounds had significantly higher preference for three of the five Landscape Categories. Participants with higher levels of prairie Experience had significantly higher preference for four of the five Landscape Categories. Those with higher prairie Knowledge had higher preference for all five Landscape Categories.

Table 1. Occurrence of significant differences in mean Preference of Prairie Landscape Categories as a result of the Familiarity Variables.

Study I

Familiarity variables	*Significant difference in mean preference*				
	DH	*FG*	*W-hC*	*FT*	*WD*
Background	.001	.001	NS	NS	.05
Experience	.001	.001	NS	.001	.001
Knowledge	.05	.001	.05	.01	.05
Predisposition:					
Grassland	.001	.001	.001	.001	.001
Nature	.001	.001	.001	.001	.005
Urban	.01	.005	NS	NS	.01
Passive Stress-Release	NS	NS	NS	NS	NS
Social-Nature	NS	NS	NS	NS	NS
Social-Concern	.005	.001	.001	.001	.001

Notes: Prairie Landscape Categories: DH = Distant Hills; FG = Foreground Grass; W-hC = Warm-hued Color; FT = Foreground Texture; WD = Wooded Draws. Significance Level = .05.

In terms of Predisposition, three categories merit attention. Participants with high Predisposition for Grassland settings and natural (Nature) settings had significantly higher preference for all Landscape Categories. Those people with high Predisposition for Urban settings had significantly lower preference for three of the five Landscape Categories. The Passive Stress-Release Category (those who enjoy sleeping, watching TV, just sitting around, etc.) and the Social Nature Category (those who enjoy partying, conversation, beachcombing, etc.) had no effect on preference. The final Predisposition Category, Social-Concern (those with greater concern for social and environmental problems), was influential on preference for all Landscape Categories.

Study II

Study II involved a manipulation meant to influence Knowledge, with the possibility that increased Knowledge might influence preference. Tables 2-5 display the effects of the educational treatments on mean Knowledge levels. Tables 2 and 3 show a significant difference in mean Knowledge for the ecological and cultural/historical treatments, respectively. As anticipated, the treatment effects dissipate toward the latter part of the two-week testing period. Also as anticipated, there were no significant effects on Knowledge for the control treatment (Table 4). Table 5 shows the effect of all three treatments with test times combined.

Table 2. Effects of test time on mean Knowledge for ecological treatment.

Treatment: ecological

Test time	*N*	*Mean Knowledge*	*F-Stat.*	*Sig.*
1 day	43	5.98	2.57	.05
2 days	20	6.30		
7 days	13	5.23		
10 days	23	4.00		
14 days	12	4.50		

Table 3. Effects of test time on mean Knowledge for cultural/historical treatment.

Treatment: cultural/historical

Test time	*N*	*Mean Knowledge*	*F-Stat.*	*Sig.*
1 day	19	7.89	3.36	.05
2 days	4	7.25		
7 days	21	6.86		
10 days	5	3.20		
14 days	4	5.25		

Table 4. Effects of test time on mean Knowledge for control treatment.

Treatment: control

Test time	*N*	*Mean Knowledge*	*F-Stat.*	*Sig.*
1 day	10	3.50	.98	NS
2 days	4	5.50		
7 days	4	5.50		
10 days	13	4.92		
14 days	8	3.75		

Table 5. Effects of treatments, with test times combined, with mean Knowledge.

Treatment	*N*	*Mean Knowledge*	*F-Stat.*	*Sig.*
Ecological	111	5.38	8.06	.001
Cultural/historical	53	6.79		
Control	39	4.44		

Tables 2-5 show that the educational treatments had a limited impact on increasing prairie Knowledge level. Analyses of these treatment groups on preference, however, revealed no effects of the treatments on preference for the Landscape Categories. This result is not really surprising given the mild manipulations and given the functional importance of landscape preferences. Preferences are not trivial; if they were easily changed, our world would be a less stable one.

An important point to note is that even the control group showed some Knowledge of prairies (Tables 4 and 5). Because this Knowledge did not come from the educational treatments (control group received no treatment), it might be called previous Knowledge. The next step examined the effects of this previous Knowledge for all Study II participants, along with the other familiarity aspects on preference for the Landscape Categories. In this respect, Study II replicates Study I.

The relationship of the familiarity variables to preference for the Landscape Categories for Study II is shown in Table 6. As in Study I, a rural Background accounted for significantly higher preference, this time for four of the five Landscape Categories. There were two composite measures of Experience and both proved influential in preference for all Landscape Categories. Experience-Setting was a general measure of Experience with prairie, savanna, and farmland settings. Experience-Identify, a more stringent measure, asked participants to identify plants and animals common to prairies. As Table 6 shows, the more stringent Experience measure had a greater influence on preference levels. Participants with high prairie Knowledge had higher preference for all Landscape Categories. The Predisposition Categories' influence on preference was much the same as seen in Study I.

Table 6. Occurrence of significant differences in mean Preference of Prairie Landscape Categories as a result of the Familiarity Variables.

Study II

Familiarity variables	*Significant difference in mean preference*				
	DH	*FG*	*W-hC*	*FT*	*WD*
Background	.054	.01	.05	.05	NS
Experience - Setting	.05	.05	.001	.001	.05
- Identify	.001	.001	.001	.001	.005
Knowledge	.001	.005	.05	.001	NS
Predisposition:					
Grassland	.001	.001	.001	.001	.001
Nature	.001	.001	.001	.001	.001
Urban	.01	.005	NS	NS	NS
Passive stress-Release	NS	NS	NS	NS	NS
Social-nature	NS	NS	NS	NS	NS
Social-concern	NS	NS	NS	NS	NS

Prairie Landscape Categories: DH = Distant Hills; FG = Foreground Grass; W-hC = Warm-hued Color; FT = Foreground Texture; WD = Wooded Draws. Significance Level = .05

A comparison of Tables 1 and 6 shows that the results from both studies are quite similar and supportive of each other. A significant point is that the results for both studies for the first two Landscape Categories Distant Hills and Foreground Grass, are virtually identical. These were the two least preferred categories; thus, they clearly show the impact of the familiarity variables on preference. Together, the results of the two studies support the conclusion that the various aspects of familiarity are significant and important factors in the preference of prairie landscapes.

CONCLUSIONS

Two conclusions that can be drawn as a result of this work are 1) Familiarity is positively related to preference for the prairie landscapes studied and 2) Familiarity level deserves consideration in the aesthetic assessment, management, and design of prairie landscapes.

Familiarity was clearly and positively related to preference in the current work. This positive relationship may appear obvious to some readers yet the opposite relationship would also make sense; remember the adage, "familiarity breeds contempt." A positive relationship between familiarity and preference does not occur for every landscape and should not be taken for granted when it does occur. This conclusion holds exciting possibilities for prairie conservation and restoration.

Familiarity level matters in how much people like or dislike prairie. Thus, if we are to attempt to understand peoples' preferences for prairie lands, to assess these preferences, and even predict these preferences, we cannot disregard familiarity. Many of the aesthetic assessment techniques now in use derive from those developed in the western United States by the federal land management agencies. These techniques make use of artistic principles and expert judgement (Brown et al. 1986, Kaplan 1979, Miller, 1984). Generally, they do not measure observer attributes, and when applied to open landscapes, they find little of aesthetic value. One of the premises of this study has been that preference for certain landscapes may be greatly influenced by the observer's familiarity with that landscape. The current work shows evidence that this is indeed the case for prairie landscapes. Therefore, if we are to develop aesthetic assessment techniques that seek to measure the aesthetic value of prairie landscapes, it would appear that these techniques must take observer familiarity level into account.

It is critical that aesthetic assessment procedures be developed for prairie and other open lands with similar visual characteristics. For if we cannot measure their aesthetic value, we cannot hope to protect this value from loss. The dangers are real, whether they be suburban sprawl, agribusiness, mining of resources, disposal of dangerous wastes, or whatever else may come along in the coming decades. As our population continues to grow and to shift location, the open lands will come under increasing pressure. While few would argue for complete preservation of all open lands, doesn't it make sense to try to find ways of measuring or predicting the scenic value of these lands? This would insure that when land-use decisions need to be made, there is something to discuss besides economic expediency.

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RECONSTRUCTED PRAIRIE AS AN EDUCATIONAL TOOL

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Abstract. The southernmost extension of the tallgrass prairie of the Great Plains, called the Blackland Prairie, constitutes one of the ten major vegetation zones of Texas. Today, less than 1% of the original Blackland Prairie remains relatively undisturbed. To show visitors what a prairie looks like and to serve as an outdoor classroom and demonstration of a prairie landscape, a small section of the grounds of the National Wildflower Research Center in Austin, Texas, was planted with species salvaged from a nearby prairie remnant destined for development. Additional container-grown prairie plants and seeds were planted and sown into the area during the next two years. Species were monitored seasonally, and some management, such as weed control and a burn, was initiated. The reconstructed prairie has sparked tremendous interest from both members and visitors. An appeal to members for funding to maintain the prairie brought in more contributions than any previous appeals. The area will continue to be studied and monitored to record long-term changes and assess management techniques.

INTRODUCTION

The tallgrass prairie of the Great Plains reaches its southernmost limit in Central Texas. Known as the Blackland Prairie, it constitutes one of the ten major vegetation zones of Texas. Blackland Prairie soils include dark, calcareous clays and gray, sandy loams (Correll and Johnston 1970). Annual rainfall averages 30 to 40 inches. The climax dominant is little bluestem (*Schizachyrium scoparium* Michx.). Other important grasses include: big bluestem (*Andropogon gerardi* Vitman.), Indian grass (*Sorghastrum nutans* L.), switchgrass (*Panicum virgatum* L.), sideoats grama (*Bouteloua curtipendula* Michx.), hairy grama (*Bouteloua hirsuta* Lag.), tall dropseed (*Sporobolus asper* Michx.), silver bluestem (*Bothriochloa saccharoides* Sw.), Texas wintergrass (*Stipa leucotricha* Trin. & Rupr.) and Texas cupgrass (*Eriochloa sericea* Munro.).

The tallgrass prairie in Texas originally stretched north to south from the Red River to the San Antonio River. Today, less than 1% of the original Blackland Prairie remains relatively undisturbed (Office of Environmental Resource Management 1986). The remaining examples most representative of climax vegetation are in upland hay meadows (Collins et al. 1975). In Travis County, the Blackland Prairie has been extirpated except for a few scattered remnants that show moderate to heavy disturbance (Office of Environmental Resource Management 1986).

Located east of Austin, Texas, the National Wildflower Research Center is situated on former Blackland Prairie that was converted into a coastal bermuda hayfield. A private, nonprofit organization, the Wildflower Center strives to increase public awareness of the importance of native vegetation and to encourage the establishment of native plants in public and private landscapes to aid in environmental repair. The Center supports a research program to study native plants and their communities and serves as a resource for individuals, agencies, and organizations working with native plants. Each year, thousands of visitors, from both in-state and out-of-state, stop by the Center.

The Center grounds offer demonstration and display plantings of native species in both traditional landscapes and more natural plant associations. These areas are used extensively in education programs for students and teachers and provide examples for professionals in the landscape industry, as well as homeowners.

In the fall of 1988, botanists at the Wildflower Center decided to initiate a prairie reconstruction project on the grounds. Since then, the prairie has served a variety of purposes and is a focal point for visitors and school groups alike.

As an educational tool, the reconstructed prairie provides a glimpse of what Blackland Prairie looked like and helps to increase public awareness and appreciation of prairie communities and their complex interactions. The prairie also offers an outdoor laboratory to teach basic botany and ecology at all levels.

As a display, the plot shows how a small prairie area can be incorporated into home or corporate landscapes. The prairie offers an alternative way to look at a landscape—as an ever-changing community of plants, as opposed to the formalized designs of traditional landscapes.

As a planting demonstration, the prairie is an ongoing study of how to reconstruct a prairie community using a combination of seeding and transplanting methods and how to manage it over time.

METHODS

The desire to include a prairie on the grounds was fulfilled in the fall of 1988 when staff botanists learned of a Blackland Prairie remnant that was scheduled for development and obtained permission to salvage some of the prairie plants on the property. Located approximately 15 mi north of the Center, the remnant was one of several sites identified and mapped by the City of Austin Office of Environmental Resource Management as containing original Blackland Prairie vegetation or component prairie species (Office of Environmental Resource Management 1986).

A triangular section (about one-third of an acre) of the Center grounds was chosen to convert to prairie. Formerly covered with coastal bermuda grass, the designated area had been graded during the construction of a parking lot in 1987. In the summer of 1987, before any anticipation of a prairie, the triangle was seeded with buffalo grass (*Buchloe dactyloides* Engelm.). Some volunteer forbs, such as Indian blanket (*Gaillardia pulchella* Foug.), seeded themselves naturally. In February 1988, while still dormant, the area was partially burned to remove excess buffalo grass thatch. In early fall 1988, bluebonnets (*Lupinus texensis* Hook.) were seeded into bare patches to visually enhance the area for visitors the following spring.

Upon deciding to put in a prairie, a mound of sandy loam soil was added to create an area of better drainage and to simulate a drier, upland habitat. During late October and early November of 1988, dominant native grasses and target forbs (especially those not available commercially) were dug from the prairie remnant and placed in large pans. An attempt was made to transfer extra soil from the original site in order to include part of the prairie seed bank and its soil microorganisms. The pans were loaded onto a truck and trailer and transported to the Center, where the plants were transplanted immediately.

To fill spaces within the reconstructed prairie and to compare the success of transplants versus seeding, additional species were planted and seeded in the winter of 1988 and spring of 1989 (Table 1).

The container-grown plants, propogated in the Center's greenhouse, were from a mixture of locally wild-collected seeds and seeds from commercial seed suppliers. The two species grown from seeds that were obtained from suppliers were sideoats grama and purple coneflower (*Echinacea purpurea* L.). Narrow-leaved coneflower (*Echinacea angustifolia* DC.), Texas grama (*Bouteloua rigidiseta* Hitchc.), and Lindheimer's muhly (*Muhlenbergia lindheimeri* Hitchc.) were grown from locally-collected wild seeds. All

Table 1. Species added to reconstructed prairie.

Transplanted (P)	**Transplanted (CG)**
Andropogon gerardi	*Bouteloua curtipendula*
Bouteloua curtipendula	*Bouteloua rigidiseta*
Bouteloua hirsuta	*Desmanthus illinoensis*
Bouteloua rigidiseta	*Echinacea angustifolia*
Bouteloua trifida	*Echinacea purpuea*
Callirhoe digitata	*Eryngium leavenworthii*
Calylophus drummondianus	*Muhlenbergia lindheimeri*
Cooperia sp.	*Petalostemum pulcherrimum*
Delphinium carolinianum	*Schizachyrium scoparium*
Dyschoriste linearis	*Sorghastrum nutans*
Eriochloa sericea	*Vernonia lindheimeri*
Erodium texanum	
Gilia rigidula	
Hedeoma drummondii	
Hedyotis nigricans	
Liatris sp.	
Muhlenbergia reverchonini	
Panicum obtusum	
Penstemon cobaea	
Salvia texana	
Schizachyrium scoparium	
Scutellaria drummondii	
Sisyrinchium sp.	
Sorghastrum nutans	
Stipa leucotricha	
Tridens muticus	
Yucca sp.	

Seeded
Bouteloua curtipendula (c)
Callirhoe digitata (w)
Elymus canadensis (w)
Lupinus texensis (c)
Schizachyrium scoparium (c)
Sorghastrum nutans (c)

P = from prairie; CG = container grown;
c - commercial seed suppliers; w = wild-collected.

were planted in the winter of 1988. Indian grass, little bluestem, ironweed (*Veronia lindheimeri* Gray & Engelm.), purple prairie clover (*Petalostemum pulcherriumum* Heller.), bundle flower (*Desmanthus illinoensis* Michx.), and eryngo (*Eryngium leavenworthii* T. & G.), also from locally wild-collected seeds, were planted in late spring.

Sideoats grama, Indian grass, and little bluestem, obtained from commercial seed suppliers, were seeded directly into sections of the reconstructed prairie in the spring of 1989. Additional forbs and native grasses were seeded and planted into the prairie periodically during the fall and winter of 1989 to fill in gaps.

In the summer of 1989, the management phase of the project began. Because the area is highly visible, much of the initial management focused on reducing some of the more unsightly exotics and weedy species, including some of the more aggressive wildflowers. Those species (Table 2) were manually thinned out or removed periodically throughout the summer to encourage the establishment of more visually desirable species.

Black plastic was used to kill aggressive weeds and bermuda grass growing under a mesquite tree in a corner of the prairie. After three months, the plastic was removed and wild-collected Canada wild rye (*Elymus canadensis* L.), a shade-tolerant, cool-season native grass, was planted. A section of the prairie was burned in January 1990 to stimulate warm-season, native grasses and forbs and to remove excess thatch.

So visitors could walk through the prairie without having to wade through tall grasses, a more inviting, low-growing buffalo grass path was created. The path was marked off by ropes to keep people from trampling the rest of the prairie. All of the dominant prairie species were labled and an explanation of the project is included in an interpretive guidebook for visitors.

Table 2. Species selectively removed from prairie from fall 1988 through summer 1990.

Species	*Common name*
Baccharis sp.	Poverty weed
Bifora americana	Prairie bishops's weed
Cirsium texanum	Texas thistle
Conyza canadensis	Horseweed
Croton sp.	Croton
Cuscuta sp.	Dodder
Cynodon dactylon	Bermuda grass
Cyperus esculentus	Nutsedge
Gaillardia pulchella	Indian blanket
Gaura sp.	Lizard's tails
Geranium carolinianum	Carolina geranium
Lamium amplexicaule	Henbit
Monarda citriodora	Horsemint
Oenothera laciniata	Cut-leaf primrose
Oxalis dillenii	Yellow wood-sorrel
Pyrrhopappus multicaulis	Texas dandelion
Solanum rostratum	Buffalo bur
Solanum elaeagnifolium	Silver-leaf nightshade
Triodanis perfoliata	Venus' looking glass
Xanthocephalum texanum	Broomweed

DISCUSSION

Contrary to the results of some restoration projects, the success rate for transplants in this study so far has been quite high—most of the species have survived two growing seasons, though not all are growing vigorously. One exception is blue sage (*Salvia texana* Torr.), which did not survive. For some species, such as Indian grass, all three methods of planting—seed, transplants from the prairie remnant, and plants grown in containers in the greenhouse—were tested and observed. Although all three methods worked well, container-grown Indian grass plants have been the most successful thus far. Sideoats grama, on the other hand, grew most readily from commerial seed.

Species diversity was much greater than expected the first growing season because of the addition of soil containing a large seed bank from the original site. Also, because the area was developed with landscaping in mind, a greater proportion of forbs to grasses than is typically found in prairie was added to capture the attention of visitors.

The January burn stimulated several species, including buffalo grass (which became much thicker and flowered earlier), sideoats grama, pink evening primrose (*Oenothera speciosa* Nutt.), lizard's tails (*Gaura* spp. L.), and sunflowers (*Helianthus* sp. L.). Bluebonnets were adversely affected by the fire, which singed vulnerable seedlings.

Center botanists will continue to monitor the prairie in succeeding years and anticipate a gradual replacement of early successional species with more of the prairie dominants. Phenological data on each species has been recorded every year. Management strategies will be designed to maintain the prairie primarily as a landscape display.

The prairie is instrumental in teaching children and adults about inter- and intraspecific relationships in prairie ecosystems, as well as general botany and plant ecology principles. Elementary school students learn about pollinators, seed types and dispersal methods, plant/animal interactions, and wildflower identification. High school students can look more closely at the prairie as a plant community and examine association between and among species, both above ground and in the soil.

For college botany students, the prairie provides a diverse group of plants to identify using keys and generates discussions on such topics as allelopathy, ecological restoration, and the invasiveness of exotic species. Horticulture students can see the prairie as an example of natural landscaping, while photography classes use the prairie for a wealth of photo subjects.

With its prominent position in fromt of the Center's main facility, the reconstructed prairie receives considerable attention from visitors, especially in the spring when most of the showiest wildflowers bloom. Because of the prairie's small size and easy access, visitors can follow the path through it and get a closer look at individual species. Frequent visitors have noticed that the prairie changes both seasonally, as different species bloom and go to seed, and over time, as some species are replaced by others. Interestingly, an appeal to members for funding to continue work on the reconstructed prairie resulted in raising more money than any of the Center's special appeals to date, which indicates the scope of public interest in prairie projects.

With the number of visitors to the Center increasing each year, more people will be introduced to the ever-changing, often subtle, beauty of the vanishing prairie and perhaps will be inspired to help save the last remaining remnants, restore a small piece of land, or incorporate prairie components into their own landscapes.

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PRAIRIE INTERPRETATION TECHNIQUES VIA FIELDTRIPS, RADIO, AND PRINT MEDIA

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Abstract. Teachers and naturalists who lead fieldtrips to prairies frequently use the traditional leader-led, show-and-tell format, primarily focusing attention on prairie plants. This interpretive technique works well when participants have had previous contact with prairies and/or plant identification experiences. To catch the attention of those without prairie experience or interest in learning about prairies, interpretive techniques engaging the emotions and involving the senses appear to be more effective. Having tried a variety of approaches with diverse audiences, I offer ideas and methods for interpreting the prairie to children, to adults (with or without previous prairie experiences), and to the homebound who are not physically on the site. Examples focus on more than the plants; they involve the whole prairie—animals, plant interrelationships, soils, climate, moisture, sounds, smells, culture, and more. Variations on "hide-and-seek" and "exploring the unknown" work well as on site interpretive techniques for all ages. Printed materials can be used to develop background or set a mood for enjoying prairies. A number of sources are given. Capturing prairie experiences on audio tape for radio transmission or for use with the homebound is a challenging interpretive technique but a well-received one. Tips for creating an effective tape are detailed.

INTRODUCTION

People acquainted with prairies consider them rare and beautiful. They see beyond the grasses and colorful flowers a complex community of plants and animals, a piece of history that we often romanticize. Robert Betz (1977) calls attention to another viewpoint, however:

> To the unitiated, the idea of a walk through a prairie might seem to be no more exciting than crossing a field of wheat, a cow pasture, or an unmowed blue-grass lawn.

A prairie can look like a weedy overgrown field, badly in need of mowing, not something one willingly walks through; it might have ticks, bugs, spiders, snakes (ugh!). Besides, it's hot, has no shade, and has no place to sit. It doesn't look like much—just grass and weeds. How then do we "turn people on" to prairies? Here are some general suggestions. Be an enthusiastic and charismatic fieldtrip leader. Point out the rarity of this almost extinct landscape. Recall pioneer experiences from literature and/or quote authors who say inspiring things about the prairie. Cite the economic value of some of the rare prairie plants and insects. Show or describe plant species characteristic of the prairie, so the first-time visitors can begin to make plant friends. Fieldtrip participants are with you on the prairie for a reason; assume they are curious and interested. Provide experiences that engage the senses or imagination, that are funny, serious, contemplative, hands-on, scary, or different. Gain their trust and respect. Tell them you won't let them get hurt. Know your audience, and tailor the activities to meet their needs.

A word of caution—frequent visits by groups of people to small and/or sensitive prairie tracts may do more harm than good. Trampling can destroy plants, encourage weeds, and disturb animal activities. Take time to discuss how precious our native flora is and how quickly it is disappearing. Ask visitors to suggest ways they can explore the prairies from their outer edges, or restrict their movements to a narrow trail mowed or marked for their passage. Some of the activities suggested in this paper should only be done on prairies that are 40 ha (100 acres) or larger, where off-trail wandering doesn't affect the entire site. Discourage picking flowers, collecting seeds, or sampling animal life, unless there is a scientific study or restoration project involved that necessitates such actions. In such cases, collecting should be done carefully and conservatively by those who know how to do it. Some visitors may want to start growing prairies in their own yards. Tell them that wild-collected seed may not germinate, and plants dug from the wild often do not survive. Provide them with names and addresses of local or midwestern nurseries and commercial growers who propagate and sell prairie plants and seeds to the homeowner.

INTERPRETATION TECHNIQUES FOR ADULTS

Even the oldest adults are still at a child's stage of learning if they have had no experience with prairies. Do concrete, hands-on activities before dealing with the abstract. Realize that not all visitors to the prairie are scientists. To catch the interest of the uninitiated adult (or child), introduce them to and involve them in some of the special features that make a prairie unique. While the following activities may seem designed for children, they were all created for and done successfully with adult garden clubs, birding folk, Audubon and Nature Conservancy groups, teachers, naturalists, artists, writers, parents, and college students.

Examples of On-Site Interpretation

These activities are in no particular order. Try whatever tickles your fancy.

1. Have people stand or lie down in the tallest tall grasses, and remind them of stories about how the grass was as tall as a man on horseback. If you don't have to worry about fire ants, feel the earth and stillness while lying amid the grasses. Listen to sounds and look at the sky.
2. Walk everyone through a prairie slough that is not too deep or wet. Discuss the value of water to the prairie and to aquifer recharge.
3. Describe a plant species vividly and name it. Then have participants try to locate it. Discuss its lore. Quote an author who may have described it well, or show some artistic renditions of the plant. Engage another sense, such as touch.
4. Find all the sensuous-feeling plants on the prairie.
5. Have people search for different species of grasses, goldenrods, asters, mints, legumes.
6. Have everyone smell a crushed leaf of an unidentified mint. Then have them smell all the other prairie mints until they find that species.
7. Look for birds on the prairie; between birds, examine and learn about plants and insects, too.
8. Study prairie insects. Watch their behavior and listen to their sounds. Watch them when they appear to be mating. Are ambush bugs copulating when they are on top of each other?
9. Find a big rock and look for evidence of bison having rubbed their itchy coats on it long ago. Stand in the trench and rub your shoulders on the smooth indentation. Capture the fantasy on film.
10. Look for crayfish chimneys near prairie sloughs. Is there water in the hole? In drier areas, search for sand-digging wasps or ground-dwelling, hairy spiders.
11. Sit down for a snack and tell true prairie stories about previous inhabitants of the land.
12. Search for prairie sound makers.
13. Begin a checklist of prairies you have visited or of prairie plants

you have seen blooming. Start a checklist of prairie birds. Note the date and location of each observation.

14. Look for plants that appear to be designed to fit or accommodate certain insect visitors, or vice versa.
15. Keep a phenological record of prairie happenings for a whole year, or more. Share your discoveries with friends.

Integrating Print Media into the Prairie Experience

Carry books by authors who write about the prairie, or write your favorite prairie quotes on cards or in a notebook. When a contemplative moment seems appropriate, have everyone sit or stand and have a reading. Here are some examples:

1. Find a hill or slightly higher portion of the prairie from which to view the wind-ruffled grass. Try to imagine the land without boundaries as you read Robert Louis Stevenson's impressions, as related by Paul Gruchow (1985):

> It was a world almost without a feature; an empty sky, an empty earth; front and back, the line of the railroad stretched from horizon to horizon like a cue across a billiard-board; on either hand the green plain ran till it touched the skirts of heaven.

For children you might read from Pam Conrad's (1985) *Prairie Songs:*

> The prairie was like a giant plate, stretching all the way to the sky at the edges. And we were like two tiny peas left over from dinner, Lester and me. We couldn't even see the soddy from out there… just nothing in a big circle all around us.

2. Look for the "devil's darning needles" of needle grass and throw darts. Read what David Costello (1969) wrote about this plant:

> …the 'devil's darning needles' produced each year by the needlegrasses made excellent darts for throwing at people's clothing. I discovered early how the awns, or bristles became twisted when dry and how they squirmed and uncurled when I breathed on them. Years later, I learned that this mechanism literally plants these grass seeds by screwing them into the ground as the weather changes from wet to dry and back to wet again.

3. Lead an art trip, photo safari, or writing excursion to the prairie to capture colors, light, breeze, feel of the place. Read excerpts from Paul Gruchow's (1985) *Journal of a Prairie Year*, especially the quote about "green" on page 80.

Interpretation Via Audio Tape Recordings and Radio Broadcasts

Not everyone can physically visit a prairie. To capture the prairie experience, try creating an audio tape-recording of a walk on a prairie for radio listeners or for people in a classroom, sick room, nursing home. I did an hour-long broadcast from three prairies with host Bob Potter on the Minnesota Public Radio AM/FM network last summer. Listeners loved the program and could not detect that the program host was quite uncomfortable with the long grass and all those bugs. To make the prairie come alive for radio listeners, I pretended they were blind. I gave vivid word pictures of what we were seeing, and the radio engineer captured many of the prairie sounds using parabolas and high quality microphones and taping equipment. We recorded ourselves walking through the grass, making discoveries, rubbing scratchy leaves, smelling plants, listening to insects and other sounds, sharing prairie history, and giving readings from works by Paul Gruchow, Robert Betz, and Aldo Leopold. There was no script, but I had an outline of what I wanted the broadcast to include. When doing an audio fieldtrip, it is important to speak slowly, with evident enthusiasm and voice modulation. Spacers, such as "ah, um, silent pauses, ok's" are deadly on radio. If you would like a copy of the MPR prairie fieldtrip radio broadcast, send me a 60-minute tape with return mailer and postage.

INTERPRETATION TECHNIQUES FOR CHILDREN

What do you do with kids on a visit to a prairie? Well, I don't think they should be expected to do what most adults do when they visit the prairie—wandering around making up lists of plant species, seeing what's there, looking at the plants, saying "this is a this and that's a that," spouting Latin names. Children may very quickly start fooling around, get bored and leave, or develop a negative feeling for the ecosystem. They can learn the same things adults do, but they need to do it from a perspective based on self discovery through concrete experiences and emotional involvement, especially if compiling a species list or doing inventory is one of the goals. Usually, children, as well as the non-scientist adult, do not have much botanical knowledge. They are more interested in the animal life. Find ways to tap into that interest. Challenge children to use their math, science, and language-arts skills to investigate the prairie. Provide them with the necessary tools and resource materials, and let them make choices from the following list of activities:

1. Find the fuzziest plants. Draw or photograph them. Take a leaf sample to press for a chart.
2. Find the tallest big bluestem plants or the bluestem plant with the most stems.
3. How many prairie dropseed "mops" are there on the tract?
4. Which plants have surfaces or shapes that will most retard desiccation. Look for plants with waxy surfaces or lots of hairs.
5. How tall is the largest *Silphium*?
6. How many gopher mounds or ant hills or crayfish chimneys or spider tunnels are in or on the ground?
7. Watch, and tape record the prairie birds' songs. Find out which species is most numerous.
8. Measure to find the widest or highest pocket gopher mounds. Dig one up to see what is underneath or where the tunnel is. Find the newest mounds. Locate recent animal signs, such as tracks or scats, on the newly excavated earth. Compile a "prairie newspaper" of happenings.
9. Watch flowers for pollinators. Determine why they come to the plants.
10. Play predator/prey games in places where you won't negatively impact the prairie. Base your play on hawk/mouse, ambush bug/small bee, or robberfly/prey relationships. See if you can find some other relationship to imitate.
11. Is there poison ivy on this prairie? Does sumac or aspen live here? Ragweed? Kentucky bluegrass? Smooth brome? Provide samples or pictures of these plants (mug shots) so the private investigators, or detectives, can go to work. Look for evidence of snakes.
12. Find some cord grass or other cordage-producing grass and make some twine. Use the Chippewa Indian method of rubbing and twisting several fibers together against the leg, recounted by Densmore (1929) in a discussion on nettle and basswood twining. You might also consult someone who spins and weaves wool about the drop spindle method of twisting fibers into yarn.
13. Extract the green pigment from various plants to see how many different shades and tints are on the prairie, or match them with watercolors. Choose some other hues and do likewise. One method of extracting color is to crumple up the leaves and rub the pigment out on watercolor paper. Another way is to lay the leaf or flower petal on the paper and pound the pigment out with a rock or stick.

14. Write cinquain or haiku poetry about certain plants, animals, feelings, vistas, etc., that you experience on the prairie. The cinquain formula is five lines—the first is a title in one word, a noun; the second describes the title in two words; the third is composed of action words or a phrase about the title in three words; the fourth describes a feeling about the title in four words; and the fifth refers to or renames the title in one word. The haiku formula is three lines—five syllables, seven syllables, and five syllables.
15. Adopt a special place. Sit, stand, or lie there for 15 minutes. Record via writing or tape-recording or sketching what you experienced with all your senses.
16. Capture the sounds of the prairie on tape, using a parabola and good microphone. Capture the sights on film or by sketching or painting.
17. Look for insects mating. Note kinds, locations, positions, how long they stay engaged, which sex is biggest, where they go or what they do when mating is over, and where to find more like them.
18. Look for spiders. Try to be patient enough to see one make a kill. Tell someone what you saw, how the spider moved, how long it took for the prey to be subdued, etc.
19. Listen to the sounds on the prairie. Recreate some of those sounds in tunes or songs.
20. Try to find "Grandpa's eyebrows," "Grandma's grass," Little Blue, mop grass, black-eyed Susan, a golden stick, or other personalities or riddles on the prairie.
21. Find what you think is the rarest plant or animal on this prairie. Be prepared to tell why that is your choice.
22. Determine the "indicator plants" for this prairie.
23. What do prairie plant roots look like? How can you find out without digging up a precious prairie?
24. Write a story or play using as many prairie plant names as you can (from Roger Landers, Texas A & M University, San Angelo, TX)
25. Count all the different kinds of plants or animals in a square meter. Compare numbers with other counters. Start a species list.
26. Where is the wettest place in this prairie? How does the water get there? Where is the driest place? Why is it drier?
27. Why are there so few trees on prairies?
28. How did the Native Americans use this prairie? Which tribes visited this ground? Can you find any evidence of past human use on this tract? How old is your evidence?
29. Is there anything on this prairie that is not linked to something else on the prairie?
30. What do you like best about the prairie? What do you dislike? What is the scariest thing about the prairie?
31. What is the value of prairie, that is, what good is it?
32. Why is the North American tallgrass prairie almost all gone? What can kids do to protect what little still exists? Are we in danger of losing the shortgrass prairie?
33. Are there prairies anywhere else in the world? Are any of them in trouble?

DISCUSSSION

Nearly all the fieldtrip ideas and techniques described here engage the senses and emotions. These experiences will be remembered and may lead to numerous actions on behalf of prairies. I hope that these techniques will focus attention on more than just prairie plants and will spark a well-rounded interest in the whole ecosystem.

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