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HIRTEENTH
IORTH AMERICAN
RAIRIE CONFERENCE

obert G. Wickett, Patricia Dolan Lewis,
llen Woodliffe, and Paul Pratt, Editors

Proceedings

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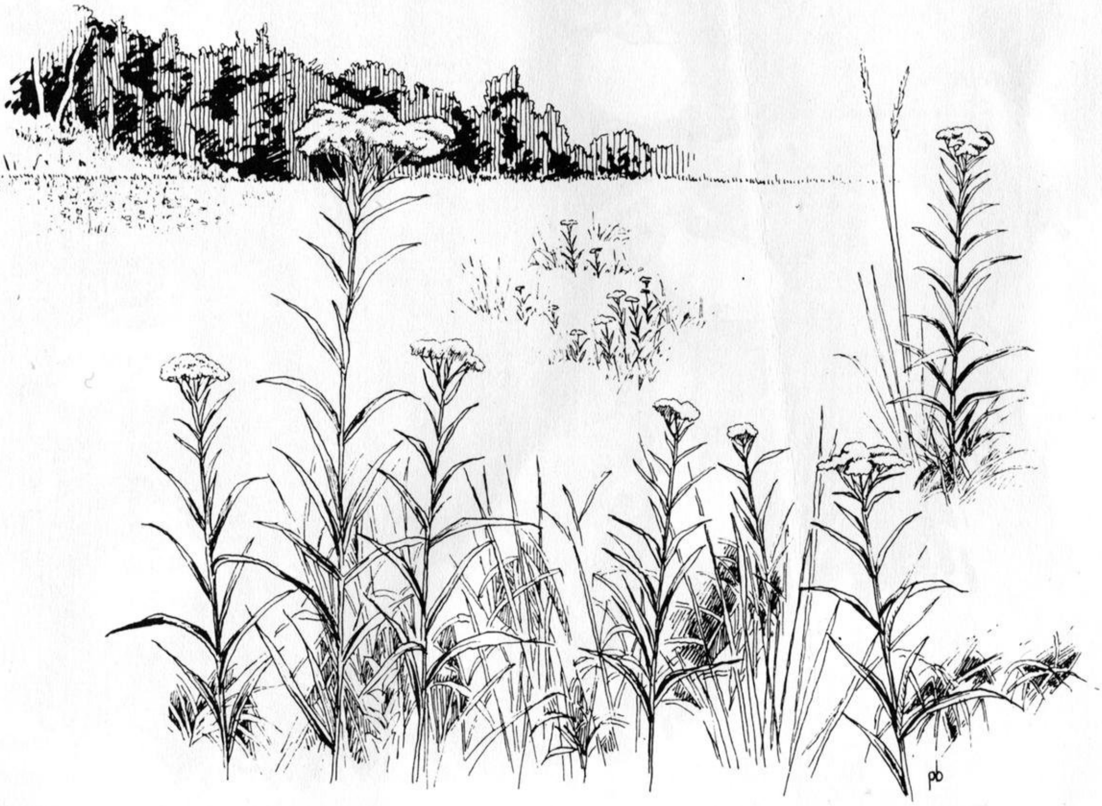
Proceedings of the Thirteenth North American Prairie Conference:

Spirit of the Land, Our Prairie Legacy



Held 6-9 August 1992
Windsor, Ontario, Canada

Chaired by
Lloyd O.W. Burridge
Edited by
Robert G. Wickett, Patricia Dolan Lewis, Allen Woodliffe, and Paul Pratt

Department of Parks and Recreation, Windsor, Ontario, Canada

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PREFACE

Unlike the prairies of the midwestern United States, the prairies of Ontario rarely stretched from horizon to horizon. Although the vastness of the prairie heartland was unfamiliar to the early inhabitants of this province, the influence of this eastern fringe of tallgrass prairie was just as significant.

The livelihood of Ontario's prairie and savannah and the native people who lived near them was so deeply intertwined that they could not survive without each other. Prairie and savannah provided a diverse plant and animal community which the aboriginals relied upon for food, clothing and medicine. In turn, the natives would burn the area in order to maintain the balance of forest and grassland as well as to protect their communities from uncontrolled wildfires. Aboriginal people considered themselves a part of the environment. If the land was healthy, so were the people that lived on it. For thousands of years aboriginal people have maintained this intimate relationship with the land on which they live.

The arrival of European settlers marked the beginning of the end for prairies. These newcomers had a different view of the land. People and the environment were separate entities and the land needed to be brought under the control of man. Prairie, with its rich soil and lack of trees, was easily tamed.

The results of these opposing viewpoints is evident in the southwestern region of this province. Walpole Island First Nation supports the finest example of tallgrass prairie and savannah in Ontario. These spectacular prairies and the native community have sustained each other for countless generations. At Windsor, the site of the Thirteenth North American Prairie Conference, another impressive prairie and savannah exists, separated from Walpole by hectare after hectare of intensive agriculture. The prairie at the Ojibway Prairie Complex survived only as a result of unique soil conditions combined with poor drainage which made it too wet for farming as well as poor economic conditions which mitigated against a steel plant complex being built on the site. The foresight of Windsor's Department of Parks and Recreation and the Ministry of Natural Resources has assured the survival of Ojibway's prairie, savanah and related forest community well into the future.

The Thirteenth North American Prairie Conference, was held in Windsor at the eastern tip of the "prairie peninsula". Sponsored by the Department of Parks and Recreation, the Ontario Ministry of Natural Resources and the Walpole Island First Nation - Council of Three Fires, this conference represented a historic moment for these meetings. Not only was it the first time the Conference was held outside the United States, it was the first time traditional native knowledge and philosophy has been incorporated into such a conference. From 6 to 9 August 1992, 273 prairie enthusiasts from 16 U.S. states and 4 Canadian provinces exchanged ideas and attitudes on the campus of the University of Windsor. In all 69 papers were presented, including 6 invited papers and 13 poster papers.

Included in the Proceedings of the Thirteenth North American Prairie Conference are 31 papers in addition to a transcript of the address by Dean Jacobs, Executive Director of the Walpole Island Heritage Centre. All manuscripts were reviewed by a minimum of one person independent of the editorial commitee. Reviewers are listed on pg vi. We offer thanks to these reviewers for their careful reviews, suggestons and prompt responses to our requests. We also wish to thank the authors for providing prompt, thorough revisions when necessary. Their cooperation and patience was much appreciated throughout this process. Thanks also go to Dr. Robert M'Closkey, University of Windsor, for his helpful advice and guidance. A heartfelt thank you goes to the many volunteer committee members who contributed their time unstintingly to ensure the success of the conference. Finally, a special acknowledgment goes to Maggie Acheson, Managing Editor, who spent long hours reviewing text, typesetting manuscripts, and designing the look of this publication. The final product is a direct result of her hard work and expertise.

Lloyd Burridge

Lloyd O.W. Burridge, M.Sc.F., R.P.F.

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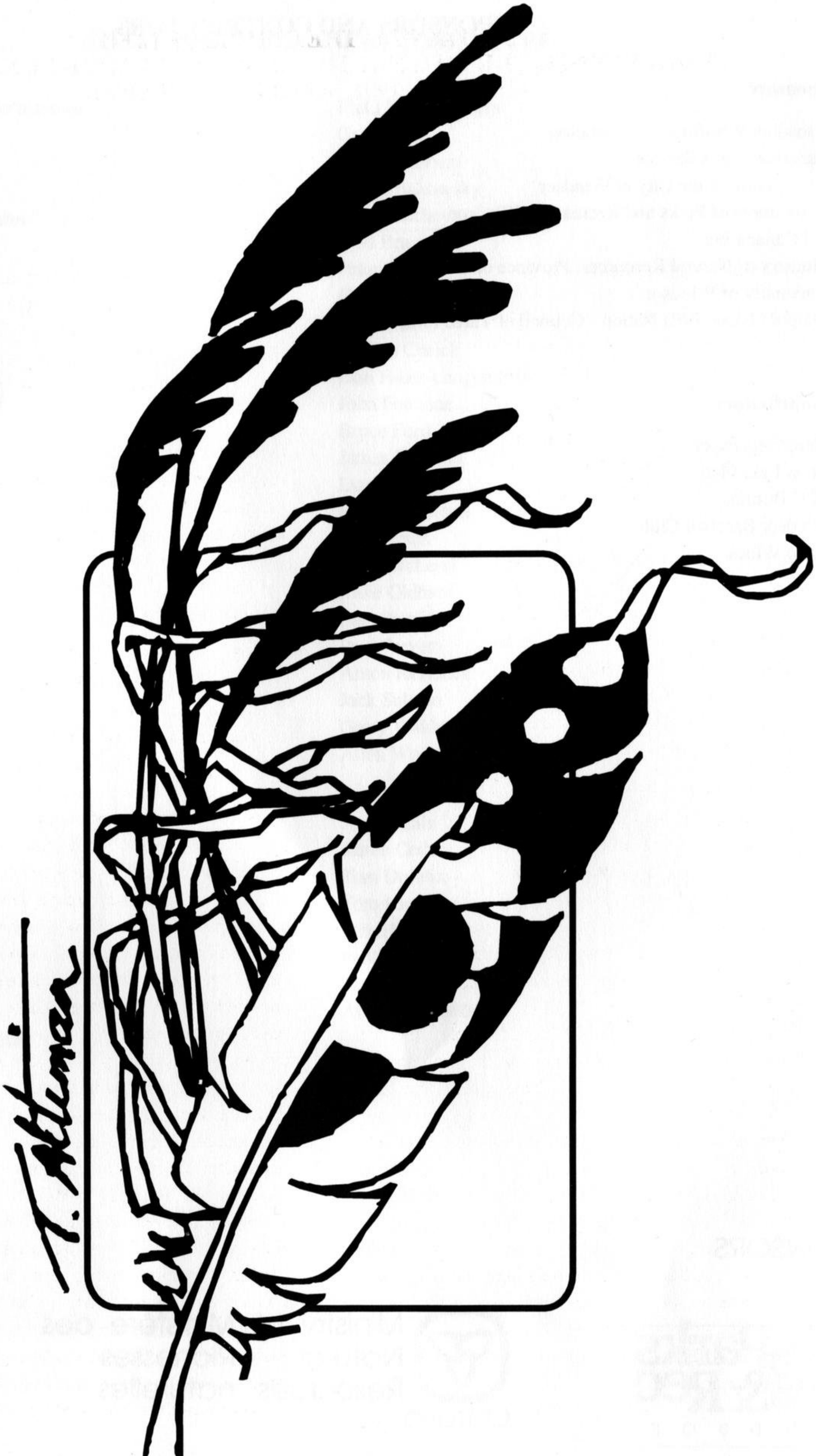

T. Altman

SUSTAINING THE CIRCLE OF LIFE
AN ADDRESS TO THE 13TH NORTH AMERICAN PRAIRIE CONFERENCE
AUGUST 7, 1992, WINDSOR, ONTARIO.

by Dean M. Jacobs
Executive Director, Walpole Island Heritage Centre

Good Morning Ladies and Gentlemen

I, too wish to bring you greetings from the The Walpole Island First Nation - the home of the modern Indian self-government and the soul of aboriginal territory.

Let me first say a few things about the conference itself. As you may know, the Walpole Island First Nation also known as The Council of Three Fires is one of the Conference sponsors. We have also been actively involved in this truly North American event.

Personally, I would like to acknowledge and thank the other sponsors, Windsor's Parks and Recreation; University of Windsor; and the Ministry of Natural Resources, for a wonderful opportunity to work together in the spirit of co-operation. Special thanks for all those people who have agreed to participate in our conference, our contributors and especially to the hard working members of the conference organizing committee, a big thank you to each one.

What we have attempted to do by way of the conference is to demonstrate and put into practice a partnership based on mutual trust to achieve a common objective of promoting cultural sharing and understanding of our distinct natural heritage: its protection and restoration. I believe this conference will lay the foundation which will strengthen relationships and open doors for future joint ventures amongst other governments, peoples and institutions. Thus, the conference theme "The Spirit of the Land: Our Prairie Legacy" is culturally appropriate and politically correct. The blending of an aboriginal presence weaving throughout the programme is no mistake. I have been to very few conferences where native people are front and centre. Usually, we are an after thought or a token add-on. Ordinarily, I am not often given a chance to keynote to such a lustrous group as we have here today from all parts of this continent we call turtle island. In the past, I would have to convene our own conference and then invite myself to give a paper. Fortunately, those days are over. That is why I am glad to be here in my own right as an equal to speak to you today. We have come a long way in removing obstacles which limited our freedom to live our own lives fully. Perhaps we can now move ahead together from this junction in time.

What I propose to do in my short time up here is to talk briefly about: The Walpole Island Community; then discuss traditional knowledge and land from a native perspective; followed by the subject of self-government; and conclude by pulling those thoughts into some semblance for future direction.

So let me begin with a glimpse of life on Walpole Island. Our reserve is nestled between Ontario and Michigan at the mouth of the St. Clair River. Occupied by aboriginal people for thousands of years, it is today home to 2,000 Ojibwa, Potawatomi and Ottawa. Having a common heritage, we formed the Three Fires Confederacy — a political and cultural compact that has survived the test of time.

The "Island" is blessed with a unique ecosystem including sixty-nine hundred (6,900) hectares of the richest and most diverse wetlands in all of the Great Lakes. Actually, the reserve consists of five principal islands with Walpole being the most prominent. At present, the reserve contains a total of fifty-eight thousand acres. Of course, Walpole Island is also known for its rare flora and fauna. You'll hear and see more of this later on this morning and tomorrow. Our local economy is primarily supported by recreation and tourism. Hunting, fishing and trapping is a multi-million dollar industry in our community. Even though we are the southern-most reserve in Canada, citizens of our First Nation, incredibly, can still support their families through hunting, fishing, trapping and guiding activities. These traditional activities are central to our economic base and cultural integrity. Our second largest industry is agriculture. Nearly twelve thousand acres are under cultivation. Cash crops such as corn and soya bean are mainly produced. Collectively we farm forty-four hundred acres under a cooperative we call Tahgahoning Enterprise. To give you an idea of the size of our farm operation, in the early 1980's we purchased the world's largest corn picker. At that time, there were only a handful of these monsters in North America. Ours became the first in Canada. The third ranking sector is government services or in other words, bureaucracy. In 1965, Walpole Island kicked out the Indian Agent, the first reserve to do so in Canada, thus opening the door to the modern self-government era. We started at square one — at zero level. Today our workforce numbers well over two hundred. It's what you might call a growth industry. I confess that I am one of those bureaucrats. I am part of the Nin.Da.Waab.Jig. group at the Walpole Island Heritage Centre. Nin.Da.Waab.Jig. means those who seek to find in our language. A phrase chosen that captures the essence of our work. The goals of the heritage centre are to support the efforts of council and the community to:

> Preserve and restore the Walpole Island First Nations' natural and cultural heritage within its homeland;
>
> Restore the rights, and improve the capacity, to manage and govern the Walpole Island First Nation fairly, effectively, and efficiently.
>
> Promote the sustainable development of the Walpole Island First Nation into the next century

The work of NIN.DA.WAAB.JIG can further be described as cooperative community-based research.

However, all is not right. Today our paradise is under siege. Walpole Island has been subjected to an arsenal of pollutants for decades. First, up-stream is Canada's major petrochemical and refining region called "Chemical Valley". Between 1974 and 1986, a total of 32 major spills, as well as hundreds of minor ones, involved 10 tonnes of pollutants. Since 1986, the Ministry of Environment has recorded an average of 100 spills per year.

Secondly, passing ocean-going freighters are a constant reminder that a "Valdez-type" disaster is possible. As it is, these ships are to blame for introducing the menacing and resilient zebra mussels to Lake St. Clair and our wetlands.

The purple loosestrife is another prolific foreign invader crowding out everything in its path. If only we could train the zebra mussels to eat purple loosestrife.

Thirdly, significant agricultural run off of pesticides and fertilizers is a major non-point pollution source. Our once popular beaches are closed for weeks on end because of high levels of bacteria.

And fourthly, dredging of contamination sediments in the surrounding waters poses yet another serious environmental problem. Environmental degradation has significant implication for our wildlife and its habitat, human health and well being, and economic development, which depends to a large degree on the viability of our natural resource base. Our socio-economic conditions mirror other native communities: high unemployment; high student drop-out rate; substance abuse; family violence; poor housing and ill health. These problems are symptomatic of cultural demise and economic dependency which disrupt the traditional supporting structures of the community and the family

While the beauty and spirit of Walpole Island is found in its natural resources and people, clearly our First Nation faces a great deal of stress. Yet, life goes on. The people of Walpole Island view life in a spiritual, holistic and dynamic way. We have a sense of place and community unrivalled in this area of the country. Our homeland is all we've ever known. This community profile is important to know for those of you who have signed up for the Walpole Island field trip on Saturday. When you visit our community I urge you to explore not only the floral but imagine the bigger picture. A way of life which has supported and preserved our prairies for centuries. After viewing our magnificent grasslands, I do hope you gain a better appreciation of our preservation efforts and the difficult choices with respect to development we face. I resent very much when outsiders tell us we **now** have an obligation to preserve these plants for the benefit of human kind. This kind of attitude ignores our contributions and traditional management legacy. At its worst it is racism. It implies that underdeveloped native communities, those who can least afford it, must bear the burden of previous uncontrolled and unsound development. This isn't just happening in Brazil and other developing countries; it's in our backyard, too. It really is a question of power and whether there is equitable justice. Unfortunately not everyone will be able to take the Walpole Island field trip. What we have done is brought a little bit of it to you here in Windsor. But we are much like a fish out of water. I can hardly do the Walpole Island community justice through mere words. Nevertheless I am extremely proud to be from the Walpole Island First Nation. Being my favourite topic I could talk about it all morning. I suppose one could say you can take me out of Walpole Island but you can't take the Walpole Island out of me. It is important for all of us to understand how this fits into the scheme of life. Our story is shared by First Nations from coast to coast.

Basically the story goes like this:

> For aboriginal people, traditional belief is often
> expressed by using the circle to represent life.
> Our life goal can be described as follows: We did
> not inherit a legacy from our ancestors. We hold
> it in trust for our future generations.
>
> Another way to put it:
> **Sustaining the circle of life.**

What can we do to ensure that this happens?

First, we can affirm that the goals of aboriginal people are compatible with the goal of sustainability of the wider society. By working with aboriginal people sustainability is promoted in the natural resource sector.

Secondly, by ensuring the preservation, continued wellbeing, and development of aboriginal cultures, including the opportunity for aboriginal people to determine their own model of development.

Thirdly, by fostering the sharing of aboriginal skills and knowledge in a way which contributes to the continued well-being and sustainability of all.

In my view, the keys to moving towards sustainability are traditional knowledge and self-government.

As part of a move towards sustainability, we all must begin to value natural resources more highly, use them more efficiently, and protect them more carefully.

Aboriginal communities have a model of development based on sustainable use of local resources. Aboriginal traditions support this model. Self government, the settlement of land claims, and the exercise of aboriginal and treaty rights help aboriginal people achieve their development goals.

Aboriginal initiatives such as self government also encourage a structural shift in how resources are managed. They encourage local management, and shared jurisdiction -- critical components of sustainability.

Aboriginal initiatives also encourage a shift in thinking about how resources are valued and used. Key concepts include sharing, efficient use of resources, and a wider definition of benefits.

Aboriginal people bring skills and knowledge to the development process -- in particular a deep knowledge of local ecosystems. We are in an excellent position to monitor and provide information on local ecosystem health. In addition, the juxtaposition of aboriginal knowledge and knowledge systems with mainstream science is likely to enrich the worldview of all.

Aboriginal people bring values and ideas to the development process. These include the concepts of sharing, and community use of resources. In particular, we bring a holistic worldview in which humans and everyday activities are intrinsic part of the land and the maintenance of environmental health. The juxtaposition of these values and ideas with mainstream ideas and values is likely to enrich the worldview of all.

Although there are real problems in reconciling the values and needs of aboriginal and non-aboriginal people in the difficult areas of resource access and management, initiatives already underway suggest it can be done and the results can be rewarding.

To aboriginal communities, "The Land" has social, cultural and spiritual - as well as economic - significance.

Because aboriginal people rely to a significant extent on local resources, the health of their communities and culture is tied in with the health of the local environment, the amount of access they have to resources, the amount of control they have over management of these resources, and the benefits they receive from them.

Self government, the settlement of land claims, and the exercise of treaty and aboriginal rights will help aboriginal people ensure access to and control of resources and the continued health of their local environment.

In the statement of political relationship - signed by the Ontario government and the Chiefs of Ontario on August 6, 1991, - the two parties agreed to enter into negotiations towards the implementation of self-government.

The statement commits Ontario to developing, in consultation with aboriginal peoples, policies, programs and self-determination, self-reliance, and protection of aboriginal cultures.

The statement of political relationship made it clear that negotiations with First Nations are done on a government to government basis. Aboriginal self-government establishes a new level of government, with sovereign powers that must be reconciled with existing federal and provincial powers. It will no longer be appropriate to consider aboriginal people as one of a number of stakeholder groups.

All self-government negotiations, however, deal explicitly with new structures. They involve identifying areas of land that will come under local, provincial, and First Nation jurisdiction. They involve discussion of both on and off reserve issues.

Self government negotiations do not explicitly include mechanisms to ensure the health of the local environment or the local economy. Aboriginal people, however, have stated that self government is not separable from an adequate land base and access to resources to ensure economic survival.

Land claims and other negotiations also deal in part with structural change.

Outstanding aboriginal land claims currently affect all directions of the province. In some cases, claims affect land that is presently dedicated to parks, resource extraction and other uses. In others, land subject to a claim may be dedicated to other uses before a settlement has been reached. For many aboriginal communities, settlement of these claims is the primary development issue. Settlement of land claims would eliminate uncertainly - allowing all residents of Ontario, including aboriginal people, a clearer picture of the future and a better opportunity to plan that future.

Self government will include greater recognition of the jurisdictional powers of aboriginal people and new approaches to the management of lands and resources and a range of social issues. In both areas, jurisdiction is a contentious issue. The province has stated that it supports shared jurisdiction, co-management, and preferential access for aboriginal people on Crown lands.

The implementation of self government and the settlement of land claims is likely to involve:

- Partnership in the management of local resources
- Change in the allocation of local resources
- Protection of the values of aboriginal people
- A decrease in the consumption use of resources
- Changes in the valuation of local resources
- Legislation which supports co-management and joint decision-making

It may also involve:

- The development of less consumptive economic activities such as ecotourism
- The development of value added industries

The co-management of resources is an aspect of multistakeholder, consensus decision-making. It provides a structure for developing consensus solutions to a number of resource issues, including:

1. The allocation of resource user fees
2. Reconciling vastly different knowledge systems
3. Defining "conservation"
4. Putting a more accurate value on resources (ie. sustainability requires that all those who use resources pay the full cost of their activities -- and that this cost reflects a wide range of values such as spiritual significance, maintaining cultural health, non-consumptive use, etc.)
5. And the establishment of a process for dealing with issues the parties cannot resolve.

Aboriginal people have retained values, traditions, and knowledge which are integral to living in harmony with nature.

We have a close relationship with the land and its resources which has survived, relatively intact, through centuries of colonization. Those who earn part of all of their livelihood through trapping and other harvesting activities develop a detailed knowledge of wildlife populations and local environmental conditions which is of value to resource monitoring, management and conservation. This detailed knowledge gives aboriginal people the authority to speak on behalf of the land, and to make decisions about the disposition and use of local resources.

Aboriginal people have much to teach the wider population about living in harmony with nature and in community with other people. A strong feature of our cultures is an emphasis on community, on sharing resources through good and bad times, and on group decision-making through consensus. To many aboriginal people, sustainable development implies social, cultural, and spiritual, as well as economic and environmental well-being. Although at present these values and ideas are removed from mainstream thinking about sustainability, they may in future become more widely accepted.

The preservation of the unique cultures of aboriginal people, and the sharing of their knowledge are therefore an important part of any sustainable life strategy. For this reason, too, one of the indicators of overall sustainability should be the well-being of aboriginal communities.

A sustainable growth strategy for the province must support the need of aboriginal people to maintain their cultures and create real options for themselves, their children, and their grandchildren. It must allow aboriginal communities to dictate the form their own development should take.

Aboriginal people have a vast and detailed knowledge of natural cycles and processes which can be applied to resource management and development. We recognize at a profound level that the land has cultural and aesthetic, as well as economic value, and that development has social, cultural and spiritual aspects. This models to the rest of society a way of living more in harmony with nature. And, most important, our efforts to preserve and promote our cultures and communities are forcing others towards a more sustainable approach to resource management.

A brief illustration on approaches to resource management points out real differences.

An Aboriginal Approach	**A Government Approach**
Local managers	Distant managers
Use of knowledge specific to local area	Use generalized knowledge
Holistic approach	Compartmentalized, Technical approach
People part of environment	Environment considered separate from people
Problems resolved at community level by community	Problems are resolved far away, through bureaucratic, political system

An Aboriginal Approach	**A Government Approach**
Harvesters are managers	Bureaucrats are managers
Resource territory is the same	Resource territory is not
As the life-space territory	Usually where people are living
Resources are shared by community	Resources are state assets allocated to private users

Less obvious are the problems in sharing knowledge. Aboriginal knowledge is a cultural package. The affective application of aboriginal knowledge is bound to the way people conduct their lives. It may not be possible to collect ecosystem knowledge for distant managers to use. Aboriginal ideas about conservation are not always compatible with non-aboriginal ideas. Both groups mistrust the knowledge of the other. In a sense, we all are in denial.

The implementation of the inherent right to self-government of aboriginal people is an integral part of any sustainable development strategy because it promotes co-management of natural resources and local decision-making.

Sustainable development plans should be explicitly discussed within the context of self-government consultations and negotiations.

One of the barriers to the implementation of self-government is its cost. In developing financing models for self government the parties involved should bear in mind its potential long-term economic benefits in terms of better resource management.

Those who live close to the land have a special knowledge of local ecosystems which is crucial to optimal resource management and supportive of sustainable development.

In order to close our circle and make it complete there must be a deeper mutual respect of our cultures. Only then can we build on events like this grasslands conference. There needs to be a movement that will succeed in legitimizing the authority of traditional knowledge. We need leaders with open minds, courage and boldness to see this through. Specifically we all can work towards enriching our lives and adding value by taking the following steps.

The province, aboriginal communities, and industry should work together to support the continuation of traditional harvesting and other land-based activities. Incentives could include the accreditation of trappers as wildlife managers, ecosystem monitoring agents, and specialists in habitat restoration, and the provision of harvesters with a minimum income supplement to help them stay on the land. The province should support traditional aboriginal activities by helping to create, along with industry and aboriginal people, markets for the products of these activities.

As part of a provincial system of sustainability indicators, the government of Ontario, in partnership with aboriginal people, should develop indicators to measure, and a program to monitor the well-being of aboriginal communities and the health of local ecosystems.

The wisdom of our elders must be recognized and respected. To the extent possible, traditional knowledge should be documented and codified. Regional centres of traditional knowledge should be established in native communities and supported by all sectors.

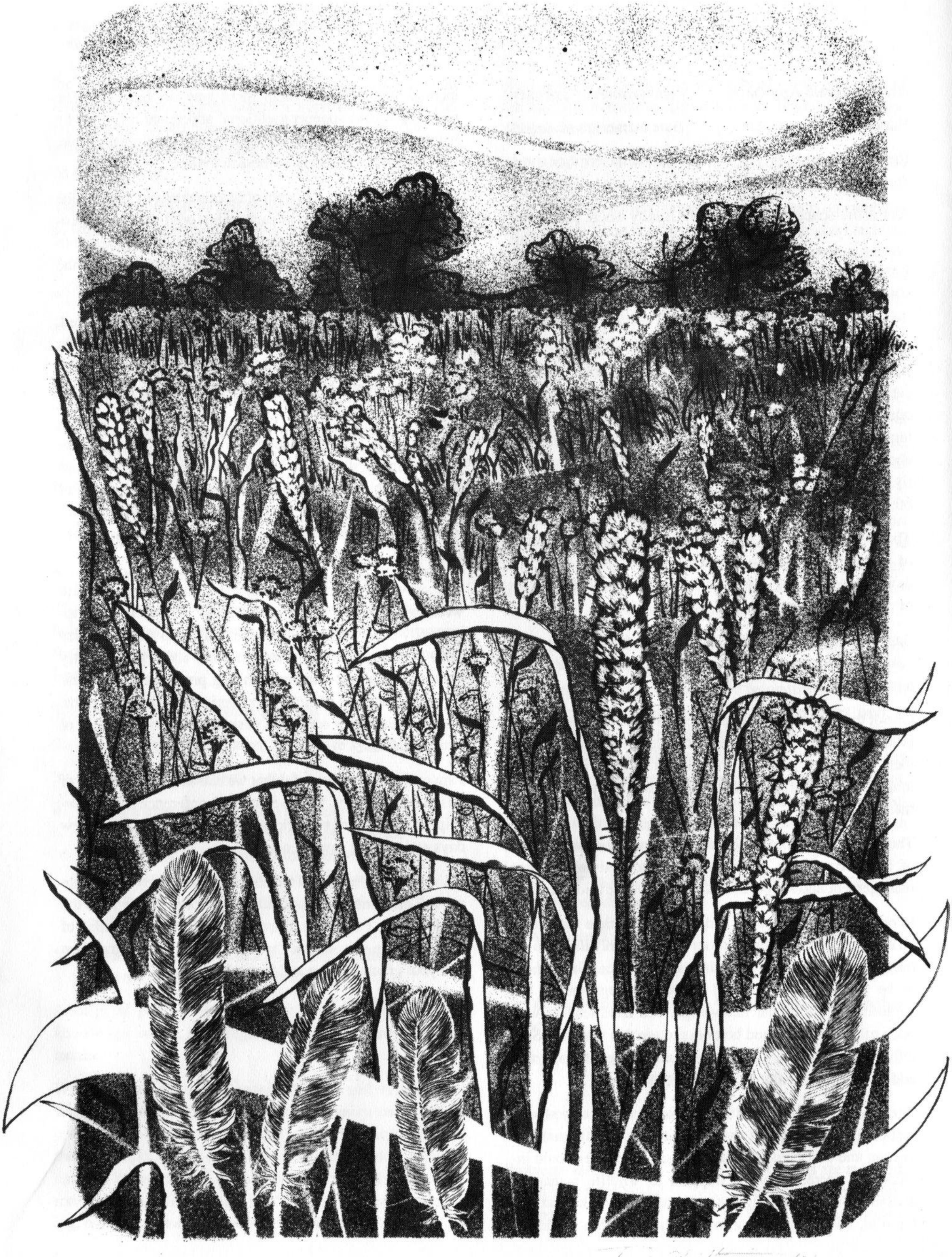
The province, aboriginal people, and industry should therefore foster the sharing of this knowledge and these values through such things as student exchanges, the inclusion of native culture in the school curriculum, and the inclusion of native people as teachers, on boards and other decision-making bodies.

The province, aboriginal people and communities should work together to ensure that aboriginal people have an opportunity to participate in the wider culture to the extent they wish to. Incentives could include joint aboriginal-industry ventures, culturally supportive hiring practices such as seasonal job sharing, culturally appropriate training programs, and post-secondary education designed to meet the needs of native students.

I am optimistic and hopeful that we can accomplish much of this in our life times. Please enjoy the conference and fellowship. I look forward to participating further over the next few days and making new friends.

So, my friends, although the circle gets larger by the minute we still have much work to do. I encourage you to keep the circle strong. For others, I invite you to cross that bridge of faith and help us continue the circle of life for my grandson and your grandchildren and beyond.

CHI-MEEGWETCH



A SURVEY OF THE PRAIRIES AND SAVANNAS OF SOUTHERN ONTARIO

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Abstract. The prairie peninsula extended into southern Ontario, and large prairie outliers were described by early surveyors and botanists. They were frequent in the near-shore areas of the lower Great Lakes, near Windsor, Chatham, Lake St. Clair, Walpole Island, Leamington, Turkey Point, and Toronto. They also occurred at inland sites, such as near London, St. Thomas, Delhi, Brantford, Dumfries Township, Lake Simcoe, Rice Lake and Peterborough. The coincidence of some prairies with portages, ancient lake bluffs and camps suggest that aboriginal peoples' use of fire, as well as natural fires and warmer- and drier-than-normal site conditions, played a role in the persistence of prairies here. Paleoecological studies show that the oak savannas that attracted some of the earliest agricultural settlers developed after 6000 BP north of Lake Erie. Many of the remaining prairies have been studied in the last 20 years and, in 1992, an assessment of prairie and savanna natural areas was commissioned by the Ontario Ministry of Natural Resources. The survey will characterize the history and ecology of southern Ontario's prairies; rank, describe and map the remaining sites; identify those already protected; and recommend the most significant sites as Areas of Natural and Scientific Interest and conservation lands.

INTRODUCTION

The earliest descriptions of prairie and savanna in southern Ontario suggest a scale of occurrence that is difficult to read from the modern landscape, so totally has it been converted to agricultural and urban land uses. This historical aspect of the ecology of southern Ontario is still not widely realized, and assumptions about complete forest coverage and the forest-clearing labours of early settlers remain deeply ingrained. The purpose of this survey is to review and analyze the status and extent of prairie, oak savanna and woodland vegetation in southern Ontario. Although these communities occur today mostly as tiny fragments of their original area, they continue to support a high complement of provincially rare species. In order to protect the floristic diversity and physiognomic structure existing within these remnants, many sites need to be protected.

In this study, physiographic regions of Ontario containing prairie and oak savanna are identified. Within each region, remnants are examined and evaluated, on the basis of physiognomic type, species associations, site substrate and moisture. High-quality remnants within both protected and unprotected sites are identified. Unprotected sites which contain representation of communities not present within protected sites are nominated as provincially significant Areas of Natural and Scientific Interest (ANSIs) to encourage the conservation of these remnants.

Historical References and Modern Remnants

Three hundred and twenty years ago, in 1670, Galinee mapped prairie vegetation during his voyage along the Great Lakes, noting "prairies" at the base of Long Point on Lake Erie. He also mapped "prairies seches" (dry prairies) near Brantford, and "grand prairies" (extensive prairies) along the eastern shore of Lake St. Clair and Walpole Island (Lajeunesse 1960).

Sarnia - Windsor Area (St. Clair and Detroit Rivers, Lambton and Essex Counties)

In 1679, the explorer Louis Hennepin wrote of the lands along the Detroit and St. Clair Rivers:

> The banks of the streight are vast meadows, and the prospect is terminated with some hills covered with vineyards, trees bearing good fruit, groves and forests, so well disposed that one would think nature alone could not have made, without the help of art.
>
> Thwaites 1903

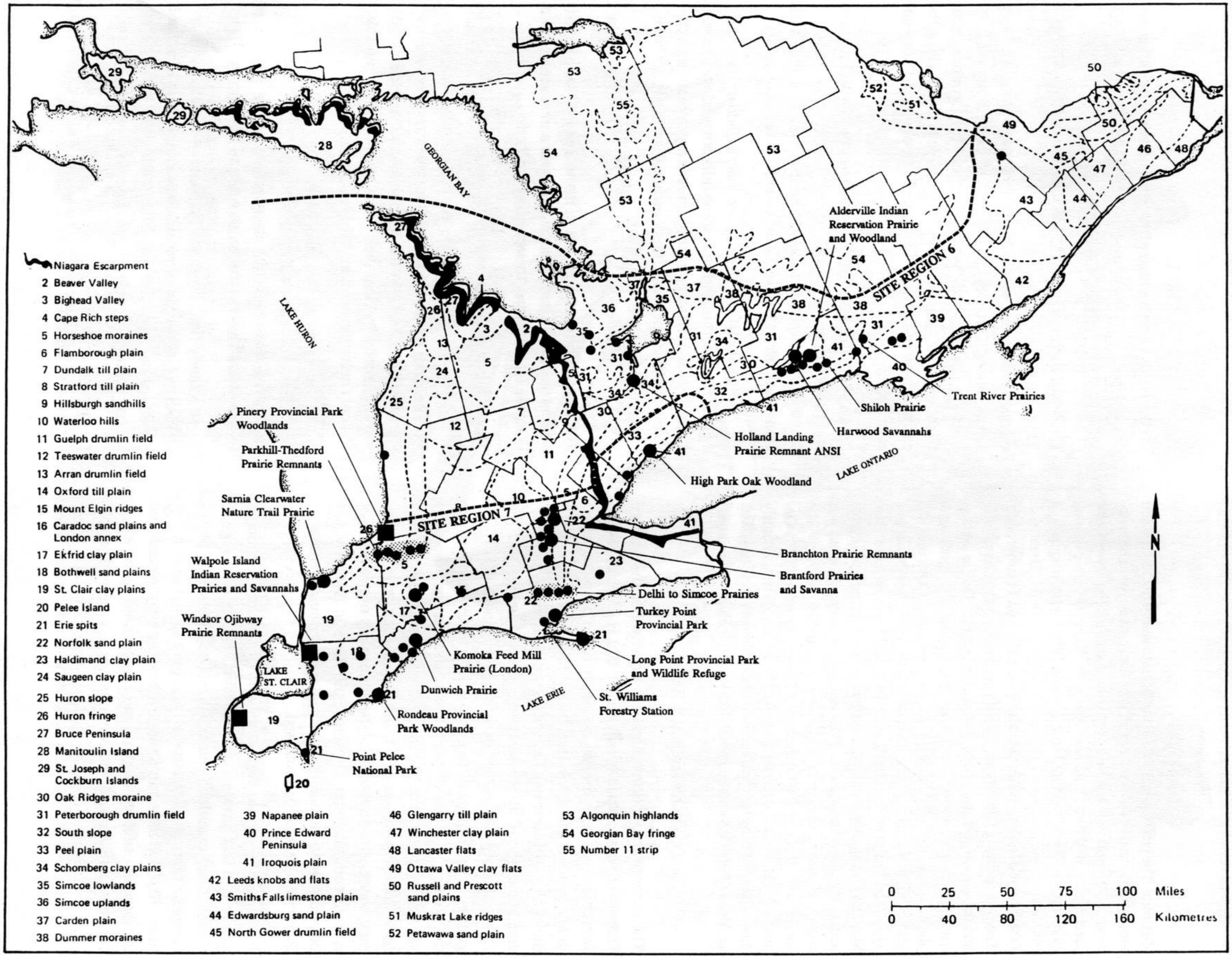
The most significant area left in the vicinity of the St. Clair river is the unequalled expanse of prairie and savanna of the Walpole Island Indian Reserve (Figure 1).

The Windsor area was visited by deLery in 1749, and he wrote:

> The lands on the east side of the river are bordered by prairies in such as way that the inhabitants have no wood to cut in order to clear their fields and sow their grain. It is only necessary to plough the land and to cut down some shrubs.
>
> Lajeunesse 1960

One of the first botanical descriptions of the prairies of southwestern Ontario was made by John Macoun in 1893:

> In a sandy field at the southern end of Sandwich [near Windsor]...a garden of rarities was entered and in a few minutes our portfolio was filled with good things. The most interesting were *Liatris spicata, Lythrum alatum,*



2 Beaver Valley
3 Bighead Valley
4 Cape Rich steps
5 Horseshoe moraines
6 Flamborough plain
7 Dundalk till plain
8 Stratford till plain
9 Hillsburgh sandhills
10 Waterloo hills
11 Guelph drumlin field
12 Teeswater drumlin field
13 Arran drumlin field
14 Oxford till plain
15 Mount Elgin ridges
16 Caradoc sand plains and London annex
17 Ekfrid clay plain
18 Bothwell sand plains
19 St. Clair clay plains
20 Pelee Island
21 Erie spits
22 Norfolk sand plain
23 Haldimand clay plain
24 Saugeen clay plain
25 Huron slope
26 Huron fringe
27 Bruce Peninsula
28 Manitoulin Island
29 St. Joseph and Cockburn Islands
30 Oak Ridges moraine
31 Peterborough drumlin field
32 South slope
33 Peel plain
34 Schomberg clay plains
35 Simcoe lowlands
36 Simcoe uplands
37 Carden plain
38 Dummer moraines
39 Napanee plain
40 Prince Edward Peninsula
41 Iroquois plain
42 Leeds knobs and flats
43 Smiths Falls limestone plain
44 Edwardsburg sand plain
45 North Gower drumlin field
46 Glengarry till plain
47 Winchester clay plain
48 Lancaster flats
49 Ottawa Valley clay flats
50 Russell and Prescott sand plains
51 Muskrat Lake ridges
52 Petawawa sand plain
53 Algonquin highlands
54 Georgian Bay fringe
55 Number 11 strip

FIGURE 1

LOCATIONS OF PRAIRIE, SAVANNAH AND WOODLAND IN SOUTHERN REGION

LEGEND

------- PHYSIOGRAPHIC REGIONS

━ ━ ━ SITE REGION BOUNDARY

■ EXTENSIVE INTACT REMNANTS

● LARGE REMNANTS (1-2 ha>)

• SMALLER REMNANTS

SOURCE: Physiographic regions after Chapman and Putnam, 1984; Site Regions after Hills, 1966.

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Aletris farinosa, Polygala incarnata, Hypoxis hirsuta, Ludwigia alternifolia, Veronicastrum virginicum, and at least a dozen others.

The surveyor Patrick McNiff (1792) mentioned that "a sandy barrren plain" extended from the foot of Lincoln Road in Windsor south to the River Canard marshes, 18 km to the south. It is estimated that plains occupied 45 square km in this area. The best known of the remaining southern Ontario prairies are, of course, in the Windsor area, the Ojibway Prairie Provincial Nature Reserve and Prairie Remnants ANSI.

Kent County

The land surveyor Patrick McNiff described portions of Kent County in the 1790's. Inland from Walpole, near Baldoon, he described the land as prairie bordering the creeks, with wooded lands at some distance from them (Lumsden 1966). From McNiff's notes, Lauriston (1952) described the lower Thames River in Kent County near Chatham:

> On each side and for a distance of 6 miles upstream were extensive meadows and marshes without any wood except for a few scattered trees. To the Dover side the marshes and meadows extended north northeast as far as the eye could see. ...Eight miles up...on the south side in general up to near the forks, the woodland does not extend back from the Thames more than 30 acres, in many places not so far; then commenced a plain.

Robert Stevenson wrote in 1843 of the land along the Thames downstream of Chatham (Guillet 1963).

> The land on its banks is about the richest I ever saw in any country. Six or seven feet deep of earth that would do for a garden, and extensive grass plains stretching for miles into the country, without a tree save here and there a small clump like an island in the plain - the grass, particularly that called blue joint, furnishes excellent pasture and hay.

These 'meadows' were described elsewhere as, "for the most part, flooded in the spring" (Strickland 1853). Similar wet prairies occurred along western Lake Erie in a continuous strip from Sandusky Bay west and north almost to Detroit (Mayfield 1988). Little of these Kent and Essex prairies remain. Small remnants are present at Rondeau Provincial Park, and tiny ones are found along railways and river bluffs (Figure 1).

Lambton County

Along the Lake Huron shoreline and nearshore areas in Lambton County, are the oak - pine savannas and woodlands of Pinery Provincial Park and the Port Franks area. Historically, this has been the habitat of the provincially endangered Karner blue butterfly *(Lycaeides melissa samuelis)*, which may now be extirpated. Elsewhere in Lambton, an outstanding, but small prairie persists along a rail right-of-way in Sarnia known as the Sarnia Clearwater Nature Trail (Figure 1).

Middlesex County

Patrick McNiff wrote the following passage in his notes during his survey of the Thames River in the 1790's:

> In this second and principal Fork of this River, in the angle formed by the two Streams is said to be a very extensive plain quite high and dry, where had formerly been a large Indian Village.

Today, small prairie openings occur on rim crests along the Thames River valley, and along railway lines and adjacent areas near Komoka (Figure 1).

Elgin County

Sandy areas near St. Thomas were described by the naturalist William Pope in his diary of 1842:

> The oak Plains appear to be pretty much settled about here...These Oak Openings or plains as they are called are much the prettiest parts of the country hereabouts...Many spots put one in mind of an English Park....

Although no remnants are presently known from St. Thomas, they are present to the west along a railway to the west in the Township of Dunwich (Figure 1).

Regional Municipality of Haldimand-Norfolk

Eastward, small but significant areas of oak-pine woodland with tiny prairie openings persist in the Turkey Point and St. Williams areas (Figure 1). A map of this area was sketched about 1795, attributed to Mrs. Simcoe, wife of Lieutenant Governor Simcoe. It showed the route he travelled from Turkey Point to London, characterized on the map as a route "thro open woods". According to original survey notes, this area formerly supported one of the most extensive areas of dry and dry-mesic prairies in southern Ontario, rivalling those from the Lake St. Clair - Thames River basin in terms of area.

Brant County and the Regional Municipality of Waterloo

Up the Grand River, near Brantford, Dumfries Township was frequently characterized by its surveyor Adrian Marlett in 1816 and 1817 as containing "oak plains", "white and black oak plains", "open plains" and "burnt plains" (Wood 1961).

In 1824, this area was also described by Colonel Edward Talbot:

> ...There are extensive tracts of land almost wholly free from any sort of timber. Such land is commonly called

> "Plains", and is for the most part of a light sandy nature, badly watered, and greatly inferior to the timbered land. There are, however, many small tracts of this kind of a very luxuriant quality. ...From the Indian settlement on the River Ouse [near the present Brantford], to the village of Burford, a distance of nearly 13 miles there is not an acre of woodland to be seen, and yet, in this tract alone, there are at least 100,000 acres. ...They are tastefully interspersed with clumps of White Oak, Pine and Poplar-trees, which give them more the appearance of extensive parks, planted by the hand of man, than of uncultivated wilds.

The plains west of Brantford were described in 1834, by the naturalist William Pope:

> ...Timber scattered in single trees and small patches in mostly oak. Indians were formerly accustomed to set fire to the brushwood in order to clear the land that grass might more freely grow which furnished plenty of food for deer. Thus these animals were enticed from all the surrounding forest.

The side-oats grama grass *(Bouteloua curtipendula)* is especially characteristic of the present, tiny Brantford remnants, which are along old and abandoned rail lines, and the dry crests of river bluffs. Other outstanding examples are the savanna 'rough' of the Brantford Golf and Country Club, and a small perched prairie 'fen' on a groundwater seep along a glacial lake shoreline bluff (Figure 1). Although some prairie species have been collected from this area in the past, the true extent and quality of these sites have only been realized over the past 5 years.

A recent reconstruction of the presettlement vegetation of the Norfolk Sand Plain between Cambridge and Long Point (Szeicz and MacDonald 1991), based on historic survey data, mapped prairie and oak savanna on 15% of the Norfolk Sand Plain. Based on palynological evidence from a lake in an area of oak savanna, it was also concluded that savanna developed in the area between 6000 and 4000 years BP, and occurred there continuously until European settlement.

Regional Municipality of York

Eastward, on the sandy plain of postglacial Lake Iroquois around Toronto, Black Oak savannas and pine barrens dominated (Lizars 1913, Goldie 1819). Lizars wrote:

> A stunted growth of gnarled oaks did not supply the whole attraction of these Plains, and dwarf cherry, sassafras and flowering shrubs rose from a ground covered with strawberry and a profusion of flowers. All descriptions of the tract speak of the startling orange lily and the masses of perennial lupine.

Karner blues occurred with the lupines *(Lupinus perennis)* in High Park until 1926, when the savanna was sprayed with weed killer. The lupine populations are now recovering, and restoration of about 45 ha of savanna is a top priority of the presently proposed park management plan (City of Toronto 1992, Varga 1988).

In 1819, the botanist John Goldie travelled in the Toronto (York) area. Walking from Scarborough to Toronto, he "entered into what in this part of the Country the People call a Pine Plain, but what in some of the States would be denominated a Pine Barren, which is a very appropriate name for such kind of land".

Around York, he noted,

> The land is naturally dry and sandy; the summer is generally dry. After leaving York 3 miles [westward, in the High Park area], you come into a Sandy Pine Barren, which continues for five miles. This is as good a Botanical Spot as any that I ever was in. (Goldie's work two years earlier in the New Jersey pine barrens explains his familiarity with and interest in this vegetation.)

Goldie walked north up Yonge Street from Toronto to the Holland Landing, just south of Lake Simcoe.

> June 27. Having gone on slowly I arrived at what is called the upper Landing Place...and have bespoken a week's lodging here, as I expect it is a spot very interesting for the Botanist. [July 4] Since I came here I have seen a number of rare plants and some of them are nondescripts - There are a species of *Asclepias* with orange flowers very handsome *[A. tuberosa]*, a species of *Euphorbium* with white flowers *[Euphorbia corollata]*, a *Ranunculus [R. rhomboideus*, prairie buttercup, here at Goldie's type location], together with some others which were not in flower, that I had never seen before.

The Holland Landing Prairie was a native encampment often mentioned in travellers' diaries because it was the northern terminus of the portage route from the Humber Plains and High Park on Lake Ontario to the Holland River. Hunter (1948) summarized these accounts:

> The open space referred to by Galt and other early writers was used as a camping-ground by the early Indians and fur-traders. Here could be seen encamped at all seasons of the year large numbers of Indians, often from very remote districts of the upper lakes.

The Holland Landing prairie is publicly-owned, but was planted to pine a number of years ago, which must be cleared if the prairie flora is to survive there (Gould 1988).

Simcoe County

Elsewhere in the Lake Simcoe area, a few other small remnants of prairie persist, associated mostly with the sandy terraces of postglacial Lake Algonquin shorelines. These sites are probably remnants of prairie communities more widespread on the shores of the postglacial Great Lakes during the Hypsithermal climatic warming, maintained since then on drier- and warmer-than-normal sites, encouraged by the activities and the occupation of native peoples (Reznicek 1983).

Northumberland County

Eastward again, extensive oak savanna occurred on the rolling sand and kame deposits on the Oak Ridges Moraine south of Rice Lake, and on the sandy till plains and drumlins adjacent to the moraine. Catherine Parr Traill was one of Canada's first female botanists, and lived for 11 years on the south side of Rice Lake. She gained fame from books such as 'Canadian Wildflowers', 'The Backwoods of Canada' and 'Studies of Plant Life in Canada, or Gleanings from Forest, Lake and Plain'. In 1836 she wrote:

> We now ascended the plains - a fine elevation of land - for many miles scantily clothed with oaks, and here and there bushy pines, with other trees and shrubs. The soil is in some places sandy, but varies...considerably in different parts, and is covered by large tracts of rich herbage, affording abundance of the finest pasture for cattle. A number of exquisite flowers and shrubs adorn these plains, which rival any garden in beauty during the spring and summer months. Many of these plants are peculiar to the plains, and are rarely met with in any other situation. The trees, too, though inferior in size to those in the forests, are more picturesque, growing in groups or singly, at considerable intervals, giving a sort of park-like appearance to this portion of the country.

The extent of these plains was also described by Samuel Strickland (1853) in his diary, as "the Rice Lake plains, which extend for nearly twenty miles along the south shore." Strickland crossed the plains on his northward journey to the lake and beyond, noting, "For nearly three miles our road lay through natural park-like scenery, flowery knolls, deep ravines and oak-crowned hills." Recent assessment of the extent of these plains based on historical records indicates that at least 172 square km, and possibly 250-300 square km may have been present here (Catling, Catling and McKay-Kuja, 1992).

Peterborough County

The surveyor John Smith (1827) described the area north of Rice Lake.

> The townships of Monaghan and Ottonabee...form the northern shores of the Rice Lake...and sandy plains skirt the Rice Lake shore.

The Town of Peterborough, which lies 20 km north of Rice Lake, was also in an area of relatively open plains, as Smith further wrote:

> The town-lot of Peterborough...being on an elevated sandy plain.

Traill (1836) described these same Peterborough plains a little more eloquently.

> These plains form a beautiful natural park, finely diversified with hill and dale, covered with a lovely green sward, enamelled with a variety of the most exquisite flowers, and planted, as if by Nature's own hand, with groups of feathery pines, oaks, balsams, poplars, and silver birches.

Other localities in this area which harbour relict prairie and savanna vegetation or species include Pontypool to the west of Rice Lake (Varga, pers. comm.), the Trent River (Catling, pers. comm.) and Healey Falls (Dore and McNeill 1980) to the east.

Paul Catling and Vivian Brownell recently made a search for remnants of this previously discounted prairie area, focusing on areas of sandy soils at high elevations. They concluded that much of that area supported something in the order of 1 mature tree per acre, and that, by 1860, only small isolated patches remained. Today, some of the best of the tiny, remaining prairies are on native lands, as they are at Walpole.

The Rice Lake plains were encouraged through burning by aboriginal peoples, who "made a practice of burning over tracts of these plainlands to promote the growth of the various grasses on which the deer fed ... Rice Lake is still called in their language 'The Lake of the Burning Plains'" (Traill 1885).

ABORIGINAL USE OF FIRE

The relationship of prairies and savannas with aboriginal land use is documented in historic accounts of campground and portage maintenance, habitat improvement for game animals, and agricultural land clearing (above references and Wood 1958, Chanasyk 1972, etc.) Fire was the customary technique.

Indian villages and campsites with prairie vegetation have been described from Windsor, Brantford, Holland Landing, DeGrassi Point and the Rice Lake Plains. A network of foot trails criss-crossed southern Ontario, often parallel to major waterways, such as the Thames, Grand and Trent-Severn. A significant number were between waterways, such as those between Lake Simcoe and the Humber River, Hamilton west to Brantford and London, and Rice Lake to Lake Ontario. Other trails followed modern and glacial lake shorelines; the Mississauga Trail along Lake Ontario became Highway 2, Kingston Road and Danforth Avenue (Poulton pers. comm.), and others flanked Lakes Erie and Huron (Lajeunesse 1960). Trails and encampments were sites where fire was used, and several modern prairie remnants occur along them (Reznicek 1983).

Most of the historical accounts of interior prairies and savannas date from the early 19th Century, more than two centuries after the introduction of the Eurasian diseases literally decimated the aboriginal peoples and their cultures. This was also a period characterized by warring and radical disruption of the remnant aboriginal cultures of the Lower Great Lakes. It is reasonable to consider that natural and aboriginal-maintained prairies and savannas may have been even more extensive prior to first contact if such significant areas still remained after a period of a century or more of natural forest encroachment and regeneration.

RESULTS

Since prairie, oak savannah and woodland vegetation was formerly an integral part of Southern Region's pre-European settlement landscape, and their remnants today host a large proportion of the province's provincially rare flora and fauna (as well as providing valuable scientific information on post-glacial processes, climates, plant migrations, etc.), it is important that these be protected. Protection of a few such sites is not enough, as the diversity of community structure and species associations varies greatly across Southern Region. This study attempts to address this through the use of a physiographic classification to identify this diversity. The physiographic regions used in this report correspond to those delineated by Chapman and Putnam (1984). By using such a framework, both protected and unprotected sites can be analyzed to determine the degree they are represented within a physiographic region. Where vegetation types are not represented in protected sites, and are known to occur within a region, they are nominated as provincially significant ANSIs if their floristic quality, structure and extent warrants such a designation.

This report identifies twelve physiographic regions within Southern Region as containing provincially significant remnants of prairie, oak savannah or oak woodland vegetation. Eight such regions occur within Site Region 7 and five regions are found within Site Region 6. In Site Region 7, this vegetation has been identified from seven protected sites (related dune grasslands and savannahs are known from two other protected sites), and a further 9 sites are recommended as provincially significant ANSIs. In Site Region 6, one protected site is known to support some of this vegetation, and four additional sites are recommended as provincially significant ANSIs. All significant sites are listed in the following, grouped according to site region and physiographic region.

Site Region 7

Horseshoe Moraines (East)
- Protected Sites:
  none
- Nominated Provincial ANSI:
  Branchton Prairie Remnants (prairies)

Caradoc Sand Plain and London Annex
- Protected Sites:
  none
- Nominated Provincial ANSI:
  Komoka Feed Mill Prairie (prairies)

Bothwell Sand Plains
- Protected Sites:
  none
- Nominated Provincial ANSI:
  Dunwich Prairie (prairies)

St. Clair Clay Plains
- Protected Sites:
  Ojibway Nature Reserve, Prairie Remnants ANSI,
  Windsor Municipal Parks - Ojibway Park,
  Tallgrass Prairie Heritage Park, Black Oak Heritage Park
  (prairies, savannahs and woodlands)
- Nominated Provincial ANSI:
  Walpole Island Indian Reservation
  (prairies, savannahs and woodlands);
  Reaume Street Prairie (prairie)

Erie Spits
- Protected Sites:
  Rondeau Provincial Park
  (oak savannah and woodlands, prairie-like dune grasslands);
  Long Point Provincial Park and Wildlife Refuge
  (cottonwood and red cedar dune savannahs);
  Point Pelee National Park
  (dune cedar savannahs)
- Nominated Provincial ANSI:
  none

Norfolk Sand Plain
- Protected Sites:
  - Turkey Point Provincial Park (oak-pine woodland);
  - St. Williams Forestry Station (oak-pine woodland)
- Nominated Provincial ANSIs:
  - Brantford Prairies and Savannah (prairies, savannah, prairie fen);
  - Delhi-Simcoe Prairies (prairies)

Huron Fringe
- Protected Sites:
  - Pinery Provincial Park (oak savannah and woodland)
- Nominated Provincial ANSI:
  - Sarnia Clearwater Nature Trail (prairies)

Iroquois Plain
- Protected Sites:
  - High Park Oak Woodlands ANSI (oak woodlands)
- Nominated Provincial ANSI:
  - none

Site Region 6

Oak Ridges Moraine
- Protected Sites:
  - none
- Nominated Provincial ANSI:
  - Harwood Savannahs (savannah)

Peterborough Drumlin Field
- Protected Sites:
  - none
- Nominated Provincial ANSI:
  - Alderville Indian Reservation Prairie and Woodland (prairie, oak woodland)

South Slope
- Protected Sites:
  - none
- Nominated Provincial ANSI:
  - Shiloh Prairie (prairie)

Simcoe Lowlands
- Protected Sites:
  - Holland Landing Prairie Remnant ANSI (prairie)
- Nominated Provincial ANSI:
  - none

Iroquois Plain
- Protected Sites:
  - none
- Nominated Provincial ANSI:
  - Trent River Prairies (prairie)

DISCUSSION

Catherine Parr Traill wrote (1885):

> Before the plainlands above Rice Lake were enclosed and cultivated, the extensive grassy flats were brilliant with the azure hues of the Lupine in the months of June and July, but the progress of civilization sweeps the fair ornaments from the soil.

The prairies and savannas across southern Ontario were put under with great efficiency by our forebearers, and they remained largely unknown, and certainly unheralded, until the last 20 years. Some workers may have even discounted the historical literature. For example, for many years, James Herriott's collections of prairie species along the Grand River bluffs south of Cambridge were considered as too fantastic by some botanists, who rationalized them as introduced waifs along rail lines (e.g., *Silphium terebinthinaceum*).

The evidence of historic prairies remained in the geographic names of communities across southwestern Ontario. Prairie Siding, Plainsville, Fairfield Plain, "Church of the Paris Plains", Round Plains, Raleigh Plains, and Dover Plains are a few of the signposts left.

Most versions of Edgar Transeau's famous map of the prairie peninsula don't include any areas in southern Ontario, even though early versions of the map did, such as the one shown in Stuckey (1981). It included parts of the Bothwell and Norfolk Sand Plains, the St. Clair and Haldimand Clay Plains, and the Horseshoe Moraines.

To summarize, prairies and savannas were an extensive and outstanding feature of several large portions of southern Ontario. The extent of the losses of native prairie and savanna can be estimated from the few such reconstructions of presettlement vegetation, from paleoecological studies, and from estimates of the historic frequency of such ecosystems on certain soil types.

The present distribution of prairie and savanna remnants suggests the probable, pre-contact extent of prairie ecosystems. They occur principally on the sandy lake plains of modern Lakes Huron, Erie and Ontario, and, more rarely, on the shoreline bluffs of postglacial and modern lakes, and on some of the well-drained, sandy-gravelly kame moraines away from the lakes (Figure 1).

A great deal of attention has been drawn to the loss of wetland ecosystems in southern Ontario, based on estimates of 70% wetland loss since European settlement. A much greater percentage of prairies and savannas have been converted to other uses. Manitoba completed studies concluding that they had lost 99% of their tallgrass prairies (Rowe 1990).

Maps of the presettlement vegetation of southwestern Ontario, based on the notes of original lot surveyors, have been prepared by Chanasyk (1972), Catling et al. (1992), Faber-Langendoen (1984), Faber-Langendoen and Maycock (1987), Lumsden (1966), Morsink (1978), Szeicz and MacDonald (1991) and Wood (1958, 1961). A series of unpublished county maps based on the original lot surveys, has also been assembled by Peter Finlay (1978), and is stored at the Southwestern Region Office of the Ministry of Culture and Communication, London, Ontario.

Based on these interpretations of surveyors' notes, the minimum area of 'open plains' is estimated to be 530 square km in southwestern Ontario (Essex, Kent, Lambton, Middlesex, Elgin, Haldimand-Norfolk, Oxford, Brant, Waterloo, Niagara, Hamilton-Wentworth). This represents 2.4% of the surface area of the region. In the Rice Lake area, at least 172 square km, and possibly as much as 250-300 square km was present.

This minimum estimate conflicts, however, with other historical accounts and maps, such as those of McNiff (1791) and Talbot (1824) above. It is undoubtedly an underestimate of the presettlement occurrence of prairies, for a number of reasons.

In the first surveys, lot surveyors recorded oak and pine-oak forests in many areas where numerous relict prairie and savanna communities even persist now. It is likely that much of the oak savanna was termed forest by surveyors, or the distinction was not made at all. For example, when Joseph Pickering noted that girdling of trees was the customary manner of clearing land on the Long Point plains in 1831, because the trees were often thirty yards apart and easy to avoid with the plough (Guillet 1963), those lands were likely surveyed as forested or wooded, rather than open.

Wood (1961) noted that European settlers may have viewed lands described as plains with suspicion, considering treelessness as a condition reflecting sterile soils. Would lands recorded at a registry office as forested be more attractive to new immigrants? On the other hand, Wood (1961) also noted that other settlers, chiefly those born in North America or with experience here, recognized the attractiveness of land which could be directly ploughed without prior clearing.

Finally, many prairies and savannas occurred as a mosaic within a larger forest matrix, on a scale smaller than a concession. In such situations, common to the prairie-woodland ecotone, the surveyor would have likely characterized the dominant forest vegetation.

At present, approximately 2100 ha of prairie, oak savanna and woodland remain in southern Ontario, most of it located at Walpole Island Indian Reservation (450 ha), the Windsor Ojibway Prairie Remnants ANSI (320 ha), and Pinery Provincial Park (1,250 ha). Based on the minimun estimate of 530 square km of prairie and savanna in southwestern Ontario, 3.8% of the area of this ecosystem **at the time of 19th century surveys**, remains. Because the extent of this vegetation, even at the time of lot surveys, was underestimated, a more accurate estimate would be that less than 0.5% of original prairies and savannas remain. Based on similar estimates, and even fewer, smaller relicts in the Rice Lake area, it is likely that less than 0.1% of former prairie and savanna ecosystems persist there (Catling, pers. comm.).

The losses are such that the remaining prairie ecosystems perform few if any of their original landscape functions with regard to mammals, birds, reptiles, and amphibians, although they continue to function as diverse, high-fidelity floristic ecosystems. The remnant sites are so small that declines in populations of dependent butterflies, such as the Karner blue and frosted elfin *(Incisalia irus)*, which may be considered cyclic occurrences in larger ecosystems, have recently become extinction events in southern Ontario.

The prairies and savannas of southern Ontario have now been studied in considerable detail by Paul Pratt (1979), Tony Reznicek (1983), Don Faber-Langendoen (1984, 1987), Paul Maycock (1987), Wasyl Bakowsky (1988), Paul Catling, Vivian Brownell and Sheila McKay-Kuja (1992), Gary Allen, Michael Oldham, Larry Lamb, Al Woodliffe, Don Kirk, Terry Crabe, Brent Tegler, Casey VandenBygaart, and others. The conservation imperative is clear.

Critical sites, such as the Windsor Ojibway Prairie Remnants ANSI, Pinery, Rondeau, Turkey Point, and High Park and others are formally conserved as parks and reserves, by provincial agencies, by the cities of Windsor and Toronto, and by several conservation authorities and non-government organizations. Active management is being taken to encourage the health and maintenance of prairie ecosystems at these sites, but the resources available for this work are limited.

The prairies of Walpole Island are an extraordinary legacy of our native people. In the last few years, considerable efforts have been made to share our collective knowledge of this ecosystem, so that the natural heritage of Walpole continues to be woven firmly into the land decisions of those land owners.

Other efforts at prairie protection and management have been taken by Ministry of Natural Resources staff on publicly owned lands, such as the Manester Property at St. Williams (former home of the Karner blue and frosted elfin), and by private individuals, who have created and encouraged prairies. Overtures have been made by individuals, naturalists clubs and public agencies to municipalities, to argue for land use planning that is sensitive to the significance and maintenance of prairie remnants. This vigilance is very much required, especially in the case of railway lines which are being abandoned and potentially developed across the southwest.

CONCLUSION

The Ministry of Natural Resources has a project underway to assemble and review all the presently available information on the remaining prairies and savannas across southern Ontario. This report is intended to set priorities for the Ministry's conservation efforts for prairies and savannas, and to provide a useful overview and analysis for all the partners in prairie conservation.

Since the early 1980's, the Ministry has published a series of reports on the significant natural areas of each of more than a dozen site districts or ecodistricts across southern Ontario. The objective has been to identify the best remaining natural areas as a system of sites representative of the full diversity of Ontario's natural history. Some of those areas are in provincial and federal parks. The others, outside the park system, are known as Areas of Natural and Scientific Interest, or ANSIs.

As recently as the early 1980's, when the ANSI reports were done, prairies in Ontario were considered to be extremely rare and extremely small. For instance, the prairie remnants at Walpole, around Brantford, and south of Rice Lake were largely unknown to many biologists, academics and historians. As a result, prairies were not usually identified as a priority natural heritage theme in selecting ANSIs. Much better information is now available on prairies and savannas, and it is now appropriate to revisit the natural area data base for all southern Ontario, to document the best remaining prairies.

The present prairie and savanna study assembled the best available information on remnant prairie and savanna natural areas in each physiographic region (Chapman and Putnam 1984) for Site Regions (or ecoregions) 6 and 7 (Hills 1961). Sites with similar features have been compared with each other in terms of selection criteria such as diversity, ecological functions, condition and special features. They are contrasted with the dominant presettlement and modern vegetation-landform features of each physiographic region. The best sites meeting the selection criteria will be identified as ANSIs.

It is the policy of the Ministry of Natural Resources to encourage the protection of the significant natural heritage features of ANSIs. In itself, identification of a site as an ANSI confers no legal protection to a site. However, it establishes such sites as conservation priorities for the Ministry and others. Municipalities can exercise restrictive land use controls in Ontario under the *Planning Act*. The Ministry encourages municipalities to recognize ANSIs in their official plans, and, in some situations, intervenes in the planning process if an identified ANSI is compromised through developments authorized through the land use planning process.

The identification of private lands as ANSIs is not always well received by private landowners. However, experience has shown that landowner contact projects and awards do encourage more sympathetic private stewardship. In Ontario, the identification of ANSIs also enables private landowners to receive property tax rebates under the Conservation Land Tax Reduction Program.

This survey should become a useful resource document for the many individuals who are interested in the conservation of prairies and savannas in southern Ontario, and enable us to advance the conservation of the best remaining sites. The draft report has been released, and the final version will be completed and published by the fall of 1993.

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A VEGETATION ANALYSIS OF TALLGRASS PRAIRIE IN SOUTHERN ONTARIO

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Abstract. The purpose of this study is to describe the composition of tallgrass prairie in southern Ontario and compare floristic variation with stands to the west in the prairie-forest border. Sixty three stands were located, most on sand plains. Direct gradient analysis and ordination were used to analyze trends of vegetation and environmental factors. Stands were dominated by prairie grasses, especially *Andropogon gerardii* and *A. scoparius*. Species responses along the moisture gradient often resembled Gaussian distributions. Ordination by detrended correspondence analysis supported the use of soil moisture as the primary gradient since the first DECORANA axis was strongly correlated with soil water retaining capacity, as well as texture, organic matter, depth of A horizon, fire frequency, magnesium, calcium, percent sand, and stoniness. Six prairie types are described using a moisture-substrate classification. Prairie communities in southern Ontario appear to require sandy to sandy-loam soils and periodic burning and/or xeric conditions. Inter-regional comparisons of prevalent species lists indicate wetter Ontario prairies are most similar to Michigan lakeplain prairies, whereas drier prairies are most similar to Michigan's woodland prairies and mesic sand prairies and Wisconsin's savannas. Typical dominants of drier Midwest prairie, such as *Bouteloua curtipendula*, *Sporobolus heterolepis*, and *Stipa spartea* are rare in Ontario, reflecting in part a shift in the underlying moisture gradient, as well as differences in soils and physiography.

INTRODUCTION

Scattered areas of tallgrass prairie occur in the deciduous forest region of southern Ontario, often associated with oak or oak-hickory savanna (Bakowsky 1988). These plant communities are similar to others in the prairie-forest border to the west (Gleason 1917, Curtis 1959, Anderson 1983). Their occurrence in southern Ontario gives rise to questions of origin, composition, present habitat characteristics and relations to other vegetation types.

Pollen evidence indicates that many prairie species were present in the prairie-forest border since at least the end of the Pleistocene (Benninghoff 1964), but did not form a distinct assemblage until the Xerothermic, about 8,000 years ago (King 1981). The effects of this climatic change were quite widespread and may have included areas in southern Ontario (Riley and Bakowksy, in prep.). Maps of the "prairie peninsula" produced by Transeau (1935, Stuckey 1981) suggest that prairie vegetation may have extended as far north and east as southwestern Ontario (Transeau made no mention of finding any such vegetation, but he may not have visited southern Ontario, R.L. Stuckey, personal communication). Prairie species may have dispersed into southern Ontario from the southwest (Illinois, Michigan) and southeast (Ohio) (Curtis 1959, Pringle 1982).

The presence of prairies in southwestern Ontario prior to European settlement can be demonstrated with survey records (Lumsden 1966, Pratt 1979, Faber-Langendoen and Maycock 1987). Sites further east were often referred to as "plains" or "oak plains", especially along the Lake Ontario shoreline and in Brant County (Lizars 1913, Wood 1961, Langendoen and Maycock 1983, Szeicz 1989). The discovery in Brant County of *Quercus ellipsoidalis*, an oak typical of oak barrens and oak savanna (Curtis 1959, White 1983), separated by 400 km from its nearest population in Michigan, is further evidence of the open habitat that prevailed up to the time of settlement (Ball 1981). Other studies describe localities where prairie communities existed prior to settlement (Rodgers 1966, Roberts et al. 1977, Reznicek 1980, Reznicek 1983, Reznicek and Maycock 1983, Stewart 1984, Catling et al. 1992).

More recent studies of prairie vegetation in the midwest have used gradient analysis to focus on vegetation-environment relations and species distributions (Curtis 1955, Dix and Smeins 1967, White and Madany 1981, Nelson and Anderson 1982, White and Glenn-Lewin 1984).

In this study, we analyze the prairie vegetation of southern Ontario using gradient analysis to determine the vegetation and environment features of these sites. Community types are identified and compared with other prairie areas in the upper Midwest in order to clarify the compositional characteristics of Ontario prairies.

Study Area

Climate

The climate of extreme southern Ontario varies significantly between Essex county in the southwest and the central highlands region of Waterloo, Middlesex and Brant counties. The differences between Essex and Waterloo counties for a number of climatic factors are as follows (from Environment Canada 1970):

mean annual temperature °C,	Essex	10	Waterloo	6
January isotherm °C,	"	-4	"	-6
July isotherm °C,	"	23	"	19
annual precipitation (cm),	"	69	"	91
annual snowfall (cm),	"	89	"	178

Southwestern Ontario occurs within the B4 Humid Zone of Thornthwaite and Mather (Sanderson 1948), which also includes Wisconsin, Illinois, Missouri, Michigan, parts of Indiana and northwest Ohio. The moisture index for this zone indicates that water deficits may occasionally occur, but are less probable further east. Exposed ridges, south and west facing slopes, and broad unprotected sand plains are affected by the warmer than normal microclimates associated with the Great Lakes (Hills 1952, Chapman and Brown 1966).

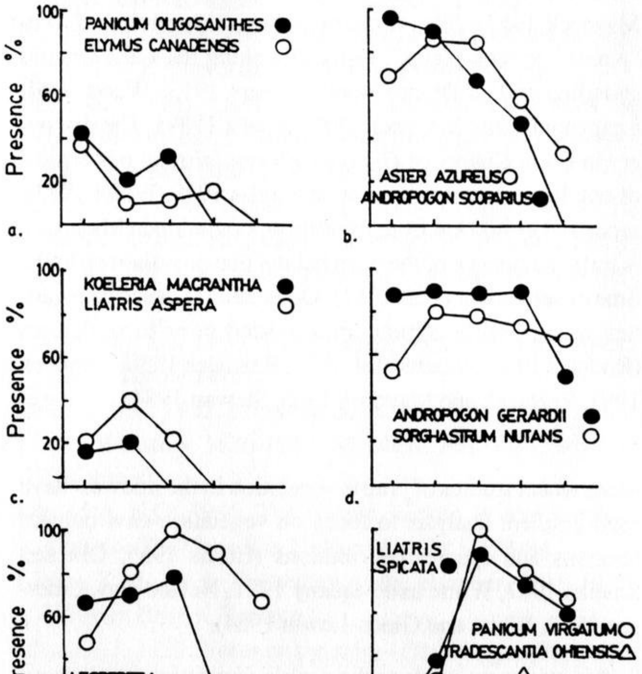

Figure 1. Representative species response curves along the moisture gradient from dry to wet in southern Ontario. Species abundance is measured as the percent presence within a moisture segment.

Physiography and soils

Almost all stands containing tallgrass prairie are located on sand plains formed as deltaic or beach deposits of 150-200 m elevation following Wisconsin glaciation (Terasmae 1980). Soils vary from coarse-textured sand at Sarnia, to silty/sandy loams at Walpole Island, to very fine sands at Turkey Point. The central highlands (360 m elevation), with more varied topography, are fringed by an extensive morainal system of till plains (Chapman and Putnam 1966). Stands of the central highlands occur on sandy loam soils over rocky substrate of the Galt and Paris till moraines and occur on steeper slopes than stands on the sand plains.

A number of stands are located along or near railways, including those at Brights Grove (railway built in 1860), many near Dumfries (railways built in 1890's) and many near the Lake Ontario shoreline (railways built in 1850's-1870's).

METHOD

Data collection

Stands were selected in 1981 and 1982 on the basis of visual dominance of grasses and forbs typical of tallgrass prairie (Weaver and Fitzpatrick 1934, Curtis 1959, Langendoen and Maycock 1983). Sixty three stands, representing a range of moisture and topographic conditions, were included (see Langendoen and Maycock Figure 1). Forty of the 63 stands had minimal human disturbance caused by plowing, grazing, or soil disturbances from railway right-of-way activities. We compiled a complete vascular plant species list for each of the 63 stands in both June and August-September. In the 40 undisturbed stands, 15 meter square quadrats were randomly laid in August and September, and species frequency and cover were recorded. In June, if spring ephemerals were abundant, 15 quadrats were laid to estimate their cover.

Soil pits 0.5 m in depth were dug to describe soil profiles in all stands. Field pH was measured with a Cornell pH test kit. Samples were collected from both A and B horizons for nutrient, moisture, texture and organic matter analyses. Stands were also visually assessed for incidences of fire and other disturbances, as well as site moisture and stoniness. Fire varied from 1 (no evidence) to 5 (burned annually during 1981-83); stoniness varied from 1 (sandy, pebbly) to 5 (rocks greater than 25 cm). A five point site-moisture classification ranging from wet to dry was determined on the basis of topographic position, substrate and degree of standing water in spring.

Soils were air-dried, broken to primary particle size and passed through a 2 mm sieve. Duplicate samples were sent to the Ontario Soil Testing Laboratory at Guelph for analyses of phosphorus, potassium, magnesium, calcium and pH. Due to costs, magnesium and calcium analyses were cut off above

Table 1. Summary of species cover values for the 5 segments of the moisture gradient. Only species attaining at least 5% cover in any one type are included.

Species	Community Type				
	Dry	Dry-Mesic	Mesic	Wet-mesic	Wet
Poa compressa	6	6	3		
Andropogon scoparius	46	31	6	2	
Hieracium florentinum	1	8			
Carex pensylvanica	2	7	3		
Aster azureus	2	6	2	1	
Solidago juncea	1	9	8	3	
Sorghastrum nutans	5	4	6	6	1
Andropogon gerardii	14	14	14	15	2
Coreopsis tripteris			5	3	
Desmodium canadense	1	1	6	3	1
Panicum virgatum		2	6	12	1
Fragaria virginiana		1	2	5	
Pycnanthemum virginianum		1	5	6	6
Calamagrostis canadensis		4	9	8	30
Solidago canadensis		1	4	10	6
Spartina pectinata			1	4	22
Aster simplex			1	1	9
Carex sartwellii				2	9
no. stands (select)	11	5	6	12	6

200 and 2000 ppm respectively, and nitrogen was analyzed in only 15 stands selected to represent the range of moisture conditions. Nitrogen was measured using the micro-Kjeldahl method. Loss on ignition at 600 °C for 4 hr was used to measure percent organic matter content. Texture of the soil fraction <2mm was determined by the hydrometer method. Hilgard cups filled with oven-dried soil were soaked until thoroughly saturated and subsequently dried for 24 hr at 105 °C to determine soil water retaining capacity, calculated as the ratio of the difference between wet and dry weights to dry weight.

Plant nomenclature follows Fernald (1950) for the dicots, Dore and McNeill (1980) for the grasses, and Voss (1972) for the remaining monocots. The vouchers have been deposited in the herbarium of the Ecology Laboratory, Erindale College, University of Toronto.

Data analyses

Percent presence (%P) was first calculated for each species across all 63 stands. Presence provides an indication of the floristic character and homogeneity of the stands because it measures the ubiquity of the component species (Curtis and Greene 1949). Frequency and average cover were calculated from quadrat data in the 40 select stands, and also averaged over all stands.

The site-moisture designations were used to organize the stand data into community types. We recognized 5 segments of a moisture gradient: dry, dry-mesic, mesic, wet-mesic and wet. We employed this site-type classification to facilitate comparisons with other regions (see below), and because a similar method is being used as part of a larger study of the vegetation of Ontario. Percent presence, mean frequency and mean cover were averaged for all stands within a segment of the gradient. Species abundances for each segment were then organized as prevalent species lists (Curtis 1959) as follows: first, the average number of species per stand within a segment was determined. Species were then arranged in decreasing order according to their presence values. The limit to the number of species on the list was determined by the average number of species per stand. For example, the 19 dry stands had an average of 59 species per stand (Appendix 1); hence the prevalent list includes the top 59 species, from 100% presence on downward. Environmental factors were also summarized for each segment.

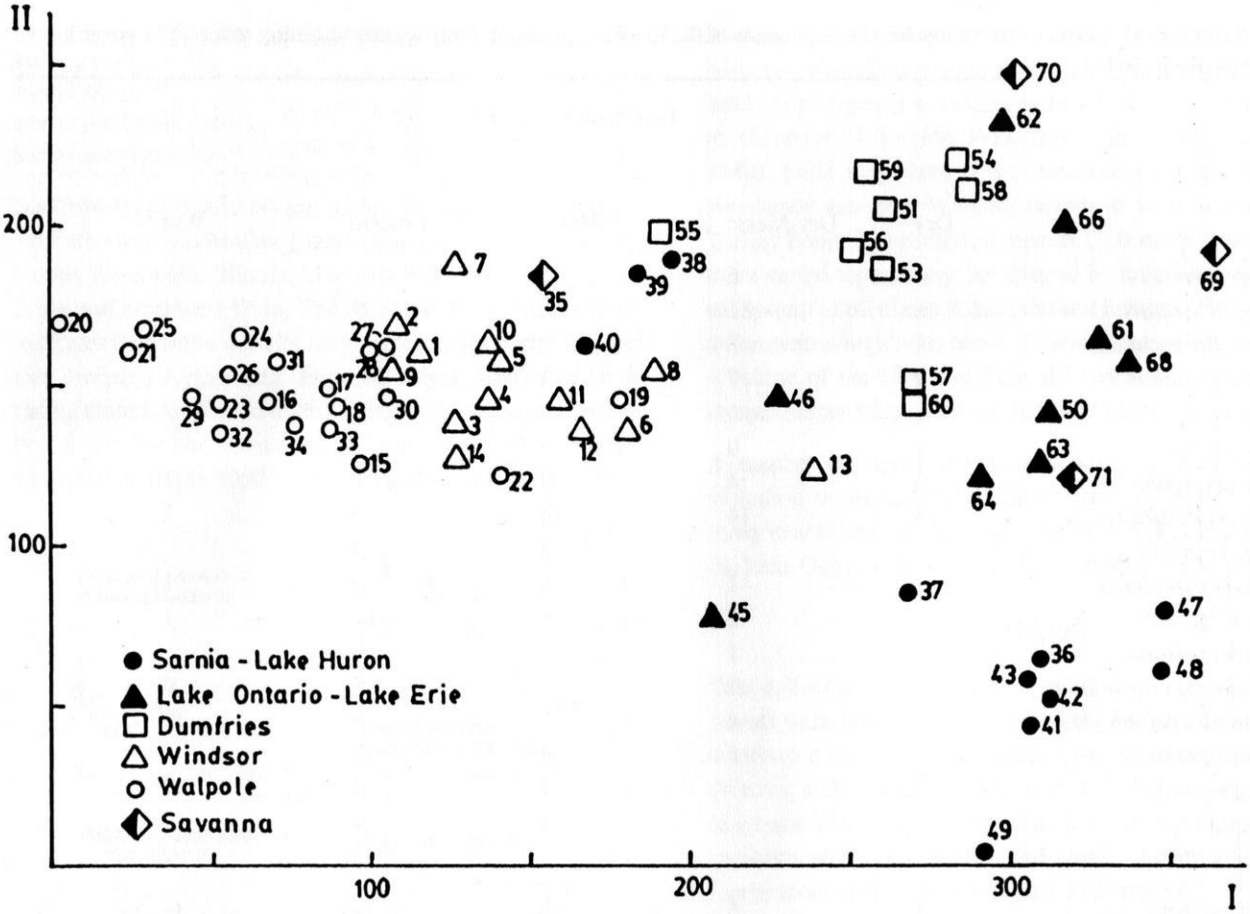

Figure 2. Detrended correspondence analysis of 63 prairie stands using species presence. Position of the 63 stands (and 4 savanna/woodland stands) on axis 1 and axis 2 is indicated by regional identifier. Numbers refer to stand locations (see text).

Detrended Correspondence Analysis (DECORANA) was used to analyze major compositional trends (Hill and Gauch 1980). DECORANA is especially useful for large, heterogeneous data sets that have strong primary gradients. The ordination model assumes a unimodal species response along gradients (Austin 1985, Minchin 1987, Peet et al. 1988). The first ordination matrix contained presence data for 322 species in 63 stands (and 4 savanna/woodland stands). The second ordination contained mean frequency data of 225 species in 40 stands and was used to test vegetation-environment relationships using Spearman rank correlations of DECORANA axes with environmental factors. Both ordinations only included species with occurrences in more than 2 stands.

Community comparisons with other regions

Data for Wisconsin prairies and sand barrens (6 types) (Curtis 1959) and Michigan prairies (7 types) (Chapman 1984) have been summarized by prevalent species lists using segments of a moisture gradient similar to that of Ontario. Prevalent species lists of Ontario prairie were first compared with these regions using the Index of Similarity developed by Sorenson (1948, in Mueller-Dombois and Ellenberg 1974). Second, a matrix of the prevalent species lists was ordinated. The matrix, which consisted of constancy values for 304 species in 18 types, was analyzed using default settings in DECORANA.

RESULTS

Composition summary

A total of 503 vascular plants were recorded in the 63 stands of Ontario prairies. Grasses were most dominant and *Andropogon gerardii* had the highest percent presence (87%) and an average cover of 13%. Other grasses with high cover values included *Andropogon scoparius* (18% cover), *Calamagrostis canadensis* (9%), *Panicum virgatum* (5%), *Spartina pectinata* (5%), *Sorghastrum nutans* (5%) *Poa compressa* (3%), and *Poa pratensis* (3%). A variety of forbs had high average cover values, including *Solidago canadensis* (5%), *Pycnanthemum virginianum* (4%), *Fragaria virginiana* (3%), *Desmodium canadense* (3%), and *Solidago juncea*

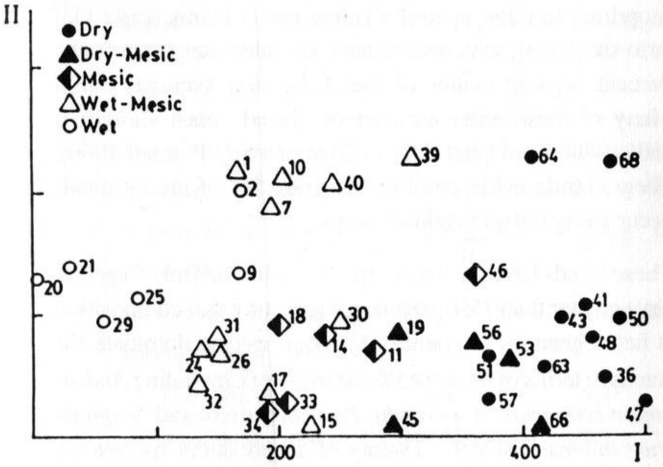

Figure 3. Detrended correspondence analysis of stands using frequency. Position of the 40 stands on axis 1 and axis 2 is indicated with symbols that refer to site-moisture designations.

(3%). Ten of the 13 species with high cover species belonged to the Poaceae or Asteraceae.

Woody plants were of minor importance in the prairies, the only widespread species being the vine *Vitis riparia* and the shrub *Cornus racemosa*. None were frequent, except locally. The tree species of highest constancy was *Quercus velutina* (38%), found most often as a seedling or sprout.

Direct gradient analysis

Presence values were plotted along the moisture gradient for several species (Figure 1). Species dominant in dry or dry-mesic stands but which occurred commonly in other moisture conditions include *Andropogon scoparius* and *Aster azureus* (Figure 1b). Several species had optima in dry or dry-mesic stands, but were of low presence and restricted to this part of the moisture gradient, e.g. *Koeleria macrantha* and *Liatris aspera* (Figure 1c).

Andropogon gerardii and *Sorghastrum nutans* had broad responses and no clear moisture preference, though they were less often found in wet stands (Figure 1d). Others, such as *Desmodium canadense*, *Lespedeza capitata*, *Liatris spicata* and *Panicum virgatum*, were most often found in mesic stands (Figure 1e,f).

Broad ranging species most often found in wet or wet-mesic stands included *Tradescantia ohiensis* (Figure 1f), *Calamagrostis canadensis*, *Spartina pectinata*, and *Carex stricta* (Figure 1h).

Species responses along the moisture gradient often resembled bell-shaped distributions. However, several species showed deviations from this pattern, including *Elymus canadensis* and *Panicum oligosanthes* in the drier stands (Figure 1a) and *Apocynum cannabinum* and *Cirsium discolor* in the wetter stands (Figure 1g). These trends were also observed when mean frequency values are used.

Dominance patterns using species cover are summarized for each moisture segment in Table 1. Prairie grasses dominate in all moisture conditions. Species richness per stand was highest in mesic stands and lowest in the dry. Stand richness (Appendix 1) and number of dominants appear to be inversely related.

Ordination

The DECORANA ordination of all 63 stands tended to group stands based on a combination of regional location and site-moisture characteristics (Figure 2). Walpole stands are separated at one end of the axis, blending somewhat with the intermediately-placed Windsor stands. All other stands are placed at the other end, but they separated strongly along the second axis of the ordination. The regional patterns retained on the ordination may reflect both distinct differences in habitat and the isolation of these prairie areas from each other.

The DECORANA ordination of select stands by species frequency is presented in Figure 3, with stands labelled according to their site-moisture designations. Stands segregated along the first axis on the basis of species composition relating to a site-moisture gradient. There was some overlap between adjacent site-moisture groups, especially for mesic and wet-mesic stands. Species locations in ordination space were comparable to their position along the direct moisture gradient (Figure 1).

Second axis variation was especially apparent among the wet-mesic stands, where 5 stands from Windsor and Sarnia (1,7,10,39,40) were separated as a group from 7 other wet-mesic stands at Walpole (15,17,24,26,30,31,32) (Figure 3). Species located in similar ordination space with the Windsor-Sarnia stands were *Potentilla simplex*, *Vitis riparia*, *Fragaria virginiana*, *Apios americana*, *Cirsium discolor*, *Carex lanuginosa*, and *Solidago canadensis*. Those associated with Walpole stands included *Aster dumosus*, *Carex meadii*, *Panicum virgatum*, *Juncus balticus*, *Viola papilionacea*, *Zizea aurea*, *Lysimachia quadriflora*, *Eleocharis elliptica*, *Liatris spicata*, and *Hypoxis hirsuta*. Dominance by *Carex foenea* and *Festuca spp.* accounted for the separation of the two dry stands (64, 68) from all the others (Figure 3).

Table 2. Spearman rank correlations between first 2 axes of detrended correspondence analysis and environmental variables.

Environmental variable	Axis 1	Axis 2
Soil water retaining capacity	-.63 *	.22
Percent sand in B horizon	.54 *	.28
Texture	-.60 *	-.30
Organic Matter	-.40 *	.26
Depth of A horizon	-.78 *	.14
pH	-.20	-.28
Fire	-.68 *	-.05
Stoniness	.53 *	-.28
Phosphorus	-.18	.25
Potassium	-.06	.03
Magnesium	-.70 *	.02
Calcium	-.44 *	-.06

* $p < 0.05$

Environmental gradients

Soil water retaining capacity, texture, organic matter, depth of A horizon, fire, magnesium and calcium were negatively correlated and percent sand and stoniness were positively correlated with the first DECORANA axis ($p \leq 0.05$) (Figure 3, Table 2).

No factors were significantly correlated with the second DECORANA axis, although texture and percent sand were significant at the $p < 0.1$ level. When percent sand in the B horizon was plotted over the ordination, changes were most significant along the first axis, as expected, but notable differences also occurred between the two wet-mesic groups that were separated on the second axis. These differences may account for the vegetational changes observed between Windsor-Sarnia prairies and Walpole prairies (Figure 3). When percent sand values were compared between these two groups, their distributions were significantly different ($U_s=35$, $p < 0.01$). Mean values for Windsor-Sarnia were 88 ± 6% and for Walpole were 57 ± 17% (Table 3). Field pH and fire index were also higher for Walpole prairies (Table 3).

Prairie types

Six prairie types were designated based on the results of the direct gradient analysis and ordination. We used the five moisture segments, with the wet-mesic segment divided into sandy and sandy loam sub-types, and two wet stands reassigned to the wet-mesic sandy type (see Figure 3). Environmental factors are summarized for the six types in Table 3.

Dry prairie

The dry prairie stands are widely scattered in southern Ontario, and occur on well drained slopes or upland stands. Soils vary from coarse, slightly acidic sand (Sarnia-Lake Huron shoreline) to more neutral alkaline sandy loams (Lake Ontario shoreline), with occasional rock substrates (Dumfries). Percent organic matter of the A horizon averages 5.6%. Many of these areas are part of glacial beach shorelines and/or stabilized sand dunes (Chapman and Putnam 1966). There is little evidence of recent fires. Ten of the 19 stands occur along railway right-of-ways.

These stands have the lowest species richness. Only 5 species have greater than 75% presence, suggesting that composition is heterogeneous (Appendix 1). Four species dominate the stands in terms of cover (≥5% mean cover), including *Andropogon scoparius*, *A. gerardii*, *Poa compressa* and *Sorghastrum nutans* (Table 1). Twenty of 59 prevalent species are prevalent only in this type (Appendix 1). This is the highest percent of distinct prevalents for any of the types.

Dry-mesic prairie

Dry-mesic prairie is often found on more elevated stands in the central highlands region or near Lake Simcoe, where sandy loam soils over rocky substrate predominate. It is also found on dry sandy ridges in the Windsor and Walpole areas. Soils of the former have high organic matter (5-12%) and slightly alkaline pH (7.6), whereas the latter have lower organic matter levels (3-6%) and moderately acidic pH (5.8). Four of the 10 stands occur along railway right-of-ways.

Sixteen species have greater than 75% presence, which suggests that dry-mesic prairie composition is less variable than dry prairie. The most prevalent are *Solidago nemoralis*, *Monarda fistulosa*, *Fragaria virginiana* and *Andropogon scoparius*. Dominant species, using cover, include *Andropogon scoparius*, *A. gerardii*, *Solidago juncea*, *Hieracium florentinum*, *Carex pensylvanica*, *Aster azureus*, and *Poa compressa* (Table 1).

Eight of 68 prevalent species were restricted in prevalence to the dry-mesic prairies (Appendix 1). Weedy introduced species occur most often in these prairies, totalling 12 of the 68 prevalents.

Mesic sandy loam prairie

These stands are virtually restricted to the Windsor and Walpole areas, where they occur on sandy to sandy loam soils. Topography is fairly level, soil pH is variable, and organic matter is similar to dry-mesic stands (4-12%). Depth of A horizon is greater than in the drier prairies. Stands on Walpole had evidence of recent fires, whereas those at Windsor did not.

Table 3. Summary of environmental factors of the 40 stands along the moisture-substrate gradient. Mean values are given with ± 1 SD. Nutrient analyses for magnesium were limited to values below 200 ppm and for calcium to 2000 ppm (see Methods). Where samples exceeded these limits, mean values are given without a SD, and means represent minimum values for these segments.

Environmental	Moisture Segment					
Factor	Dry	Dry-mesic	Mesic	Wet-mesic		Wet
				sandy	sandy loam	
% sand of B horizon	85.0 ± 16.0	67.0 ± 32.0	77.0 ± 16.0	88.0 ± 6.0	57.0 ± 17.0	62.0 ± 21.0
depth of A horizon (cm)	17.0 ± 5.0	20.0 ± 9.0	32.0 ± 9.0	34.0 ± 9.0	32.0 ± 6.0	39.0 ± 7.0
organic matter of A (%)	5.6 ± 3.1	6.1 ± 4.6	7.5 ± 3.3	10.9 ± 4.2	8.8 ± 2.8	11.2 ± 2.7
pH of A horizon	6.6 ± 1.1	7.2 ± 1.1	7.1 ± 1.1	6.8 ± 1.0	7.7 ± 0.5	7.1 ± 0.9
soil water retaining cap.	55.0 ± 12.0	63.0 ± 22.0	65.0 ± 12.0	78.0 ± 9.0	80.0 ± 20.0	79.0 ± 13.0
nutrients in A horizon						
nitrogen (%)	0.4 ± 0.4	1.1*	1.9 ± 0.7	1.4 ± 0.3	1.9*	2.1 ± 0.5
phosphorus (ppm)	16.0 ± 24.0	3.0 ± 1.0	3.0 ± 1.4	4.0 ± 0.9	4.0 ± 1.5	4.0 ± 1.2
potassium (ppm)	36.0 ± 15.0	61.0 ± 17.0	37.0 ± 14.0	58.0 ± 42.0	38.0 ± 10.0	49.0 ± 19.0
magnesium (ppm)	72.0 ± 42.0	120.0	134.0	178.0	199.0	187.0
calcium (ppm)	1094.0	1568.0	1625.0	1875.0	1996.0	1933.0
fire index	1.5 ± 0.4	1.8 ± 1.3	2.8 ± 1.6	2.8 ± 1.0	4.1 ± 0.6	3.5 ± 0.3
stoniness index	1.1 ± 1.3	2.9 ± 1.8	0.0	0.2 ± 0.6	0.0	0.0
No. of stands	11	5	6	7	7	4

* no replicates

Eight of 79 prevalent species were restricted to this type (Appendix 1). Only 4 weedy introduced species are prevalent.

Wet-mesic prairies

Wet-mesic prairies are virtually restricted to the Windsor and Walpole areas where they occur on level sandy to sandy loam soils. The water table is close to the surface, but flooding is rarely evident (Hoffman 1975, Anonymous 1979). All stands have a high organic matter (6-14%), but stands at Windsor and Sarnia have a much higher percent sand content than stands at Walpole (Table 3). These substrate differences are reflected in compositional differences (Figure 3); thus two subtypes are distinguished: wet-mesic sandy prairies and wet-mesic sandy loam prairies (note, however that for purposes of standardization with other Ontario vegetation studies and for comparison with other regions, the prevalent species list for wet-mesic prairie in Appendix 1 is retained as one type).

Wet-mesic sandy prairies

These stands have a high water table for most of the year, but because of the sandy soil, temporary droughts can occur in summer (Pratt 1979). Windsor stands are moderately to slightly acidic (pH 5.6-7.4); Sarnia stands are slightly alkaline (pH 7.8-8.0). Evidence of fire was slight at time of sampling, but Windsor stands are now under a burn management programme (Pratt personal communications).

Composition of these prairies was very homogeneous, with 33 species having >75% presence. Dominants (≥5% cover) are *Calamagrostis canadensis*, *Solidago canadensis*, *Andropogon gerardii*, *Spartina pectinata*, *Pycnanthemum virginianum*, and *Rubus flagellaris*. Thirteen prevalent species were restricted to this type, including *Agrimonia parviflora*, *Celastrum scandens*, *Cicuta maculata*, *Cirsium vulgare*, *Fraxinus pensylvanica* seedlings, *Osmunda regalis*, *Onoclea sensibilis*, *Oxypolis rigidior*, *Parthenocissus inserta*, *Senecio pauperculus*, *Sisyrinchium albidum*, *Solidago rugosa*, and *Thalictrum revolutum*.

Wet-mesic sandy loam prairie

These stands, which are part of the most extensive prairie sites in Ontario, virtually occur only on the level sand plains of the St. Clair River delta at Walpole Island. Soil pH is

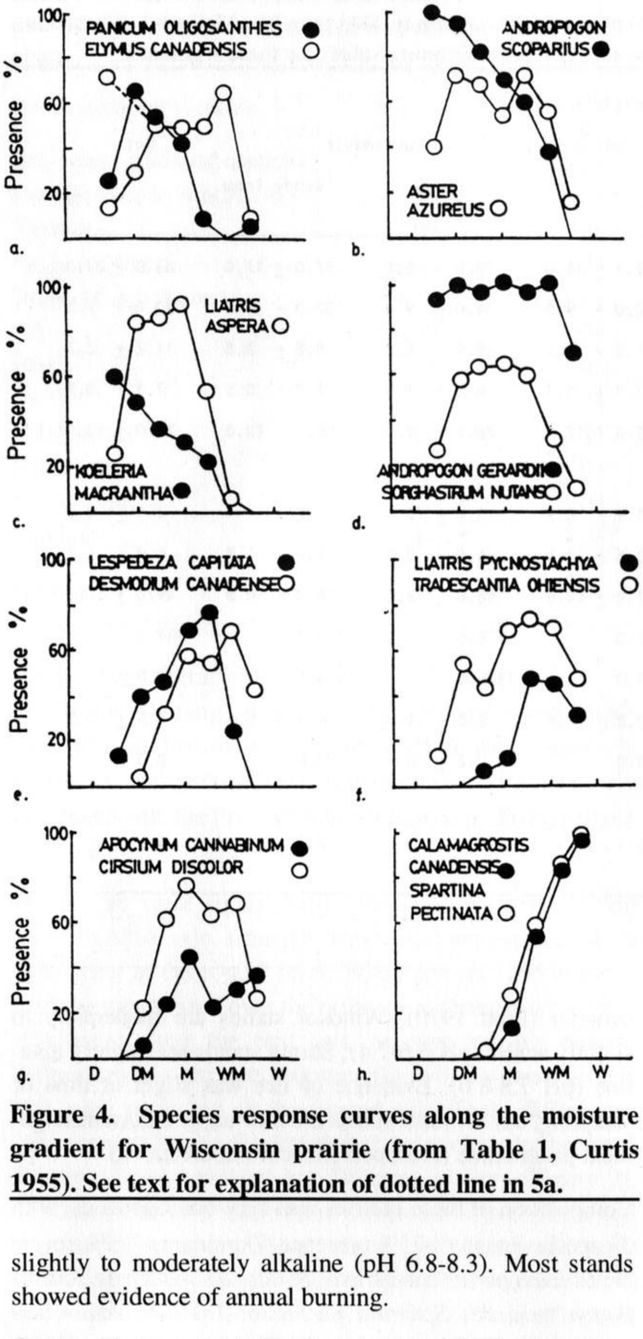

Figure 4. Species response curves along the moisture gradient for Wisconsin prairie (from Table 1, Curtis 1955). See text for explanation of dotted line in 5a.

slightly to moderately alkaline (pH 6.8-8.3). Most stands showed evidence of annual burning.

Composition was fairly homogeneous, with 24 species having a presence >75%. A number of species dominate (≥ 5% cover), including *Panicum virgatum, Andropogon gerardii, Sorghastrum nutans, Pycnanthemum virginianum, Desmodium canadense, Andropogon scoparius*, and *Fragaria virginiana*. Eleven species were prevalent only in this type, including *Aster dumosus, Carex bicknellii, Carex granularis, Erigeron philadelphicus, Erigeron pulchellus, Juncus dudleyi, Krigia biflora, Pedicularis lanceolata, Quercus palustris* seedlings, *Sisyrinchium mucronatum*, and *Tradescantia ohiensis*.

Wet prairie

These prairie stands were found only at Windsor and Walpole on level sand plains. Windsor stands were more sandy and probably less wet than those on Walpole, though both were temporarily flooded in spring. Evidence of annual fires at Walpole was high, but, because of standing water in spring, fires were also patchy.

These stands have low species richness (Table 1). Composition was very homogeneous, with 36 species having 75% presence. Dominants include *Calamagrostis canadensis, Spartina pectinata, Carex sartwellii, Aster simplex, Carex stricta*, and *Carex buxbaumii* (Table 1). Thirteen species were restricted in prevalence to this type, including *Asclepias incarnata, Carex sartwellii, Carex stricta, Carex meadii, Cirsium arvense, Galium palustre, Lythrum alatum, Mentha arvensis, Panicum boreale, Rosa blanda, Solidago ohioensis, Spirea alba*, and *Polygonum coccineum* (other apparently unique prevalents, such as *Aster umbellatus* (Appendix 1) were also prevalent in either wet-mesic sandy or sandy-loam prairies).

DISCUSSION

Composition of Ontario prairies

Prairie sites in southern Ontario contain many typical grasses and forbs of the tallgrass prairie region. Many of the characteristic plants in these prairies are rare species for Ontario (Argus and White 1977, Pratt 1979, Faber-Langendoen and Maycock 1987). Prairies in southern Ontario are most common in the southwest, especially on the Walpole Island Indian Reserve and near Windsor (Ojibway Prairie Provincial Nature Reserve), where they are associated with sandplains.

The site-moisture gradient is useful for understanding compositional trends in prairie communities in southern Ontario. The bell-shaped response curve of many species along the direct gradient suggests that moisture, in association with other correlated factors, accounts for a significant proportion of the ecological influences (Bray 1961, Nelson and Anderson 1982). The separation of stands by DECORANA ordination, which was correlated with trends in soil moisture, supported the results of direct gradient analysis.

Ordination results also indicated several secondary compositional trends that were possibly related to environmental changes in texture and percent sand. The differences in wet-mesic sandy loam soils compared to wet-mesic sandy soils supports the use of substrate for distinguishing community types, as was done for Illinois prairies (White and Madany 1981). A recent reanalysis of Curtis' data by Umbanhower (1993) also indicated that substrate was a significant influence on prairie composition.

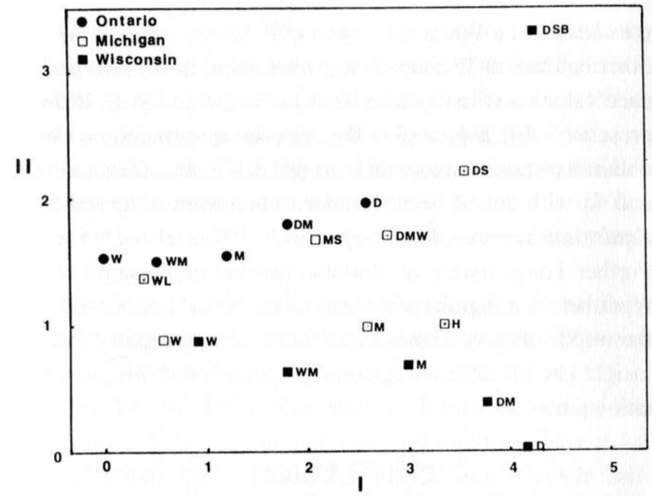

Figure 5. Detrended correspondence analysis of 18 community types in Ontario, Michigan and Wisconsin. Position of the 18 types on axis 1 and axis 2 is indicated with symbols. Ontario: W = Wet prairie, WM = Wet-mesic prairie, M = Mesic prairie, DM = Dry-mesic prairie, D = Dry prairie. Michigan: W = Wet prairie, WL = Lake-plain wet prairie, M = Mesic prairie, MS = Mesic sand prairie, DMW = Woodland prairie (dry-mesic), H = Hill prairie, DS = Dry sand prairie. Wisconsin: W = Wet prairie, WM = Wet-mesic prairie, M = Mesic prairie, DM = Dry-mesic prairie, D = Dry prairie, and DSB = Sand barrens (dry).

Plant composition of the wet-mesic loam prairies on Walpole Island differs from that of wet-mesic sand prairies at Windsor and Sarnia, particularly in the abundance of *Aster dumosus*, *Carex meadii*, *Panicum virgatum*, *Juncus balticus*, *Viola papilionacea* and *Liatris spicata* on the former. Differences between the two regions cannot be attributed solely to substrate because the fire index values for Walpole were much higher. This may account for the greater abundance of species such as *Rubus flagellaris* at Windsor.

Heterogeneity in species composition between stands increased with increasing dryness (Figure 2). Drier prairie sites are geographically more widespread throughout southern Ontario, and are quite distinct in composition from wetter prairies in the Windsor and Walpole area (Figure 2). The location of dry sites in a variety of habitats, whether inland dune systems, glacial beach shorelines, or rocky slopes indicates the unusual features needed to maintain these communities. In addition, their location along railway rights of way, and even Indian trails (Reznicek 1983) suggest that some cultural practices, whether clearing or fires, may also have maintained the open character of these sites.

Fire frequency usually increases with increasing dryness (up to a point), but the reverse trends observed here are primarily a reflection of cultural practices by residents on Walpole Island Indian Reserve, who burn many of the wetter sites almost annually. Without fire wetter sites may undergo more rapid succession to wet savanna or forest (Curtis 1959, Schroeder 1982). The importance of fire in preventing succession was observed at Ojibway Prairie Provincial Nature Reserve, where, prior to the introduction of a fire management system, prairie was succeeding to savanna and wet-mesic forest. Rates of succession in wet versus dry prairie are virtually unknown, but wetter savannas have been observed to succeed to forest more rapidly than dry (Abrams 1986).

The greater number of introduced or weedy dominants in drier compared to wetter prairies suggests that lack of fire may be affecting their composition. Fire selects against many introduced species (Henderson 1982) and favours prairie grasses (Abrams, Knapp and Hulbert 1986). Loucks et al. (1985) suggested that drier sand prairies were structurally more open and thus vulnerable to invasion, an observation also made in Iowa sand prairie (White and Glenn-Lewin 1984). The small size of Ontario sites (often less than 0.5 ha) and their location closer to agricultural fields may also increase their vulnerability.

Comparisons with other prairie regions

Comparisons of Ontario prairie to those of Michigan and Wisconsin prairie and prairie-related communities are presented in Figure 5. Wet and wet-mesic prairie in southern Ontario were most similar to lakeplain wet prairies in Michigan. Michigan's wet prairies are similar to wet and wet-mesic prairies in Wisconsin. Ontario mesic and dry-mesic prairies were most similar to Michigan mesic sand prairie. Michigan and Wisconsin mesic prairies were quite similar. Finally, Ontario dry prairie was most similar to Michigan's woodland prairie. Wisconsin dry and dry-mesic prairies were strongly separated on the second axis from Michigan and Ontario dry prairies, which showed more similarity to the dry sand prairies and barrens.

When comparing Ontario prairie to prairie-related communities in Wisconsin, the Ontario dry-mesic and dry prairie had a higher index of similarity to Wisconsin oak barrens (37%) and oak openings (38%) than to any of Wisconsin's dry to mesic prairies (24-33%). Overall the wetter Ontario prairies had greatest similarities to Wisconsin and Michigan wet prairies, whereas drier Ontario prairies showed greatest similarities to dry sand prairies and oak savannas.

Species which are prevalent in Ontario prairie and not commonly associated with those further west include *Agrimonia parviflora*, *Aster dumosus*, *Celastrus scandens*, *Gerardia tenuifolia*, *Helianthus giganteus*, *Juncus greenei*, *J. tenuis*, *Luzula multiflora*, *Panicum lanuginosum* var. *implicatum*, *Parthenocissus inserta*, *Scleria triglomerata*, *Solidago rugosa*, and *Vernonia altissima* (Appendix 1).

Species in Ontario dry prairie that are typically found in Wisconsin savannas (the "modal species" of Curtis) include *Antennaria neglecta*, *Comandra richardsiana*, *Euphorbia corollata*, *Helianthemum canadense*, *Krigia biflora*, *Lespedeza capitata*, *Lithospermum canescens*, *Lupinus perennis*, *Panicum praecocius*, *Physalis virginiana*, *Tephrosia virginiana*, and *Viola sagitta*. These species can occur as drier prairie associates, but they are most typical of savannas in the prairie-forest border (Curtis 1959). This may be a feature of tallgrass prairie at its northeastern limits. However, whereas Ontario wet prairies contain all of the grass dominants of wet prairies further west, Ontario dry prairie are often missing several significant species, including *Bouteloua curtipendula* and *Sporobolus heterolepis* of drier loam prairie in Illinois (White and Madany 1981), and *Panicum perlongum*, *Stipa spartea* and *Koeleria macrantha* in Wisconsin.

We can also compare the environmental gradient response of species in Wisconsin prairie (Figure 4) to those in Ontario (Figure 1). Wisconsin data have more intermediate points because Curtis (1955) used weighted species scores to indirectly indicate the moisture status of a stand. These graphs show a strong degree of similarity, not only in terms of the shapes of the curves, but in levels of presence. Species appear to be responding in very similar fashion to comparable moisture influences. Even those species in Ontario prairies that show bimodal trends are seen to respond similarly in Wisconsin. *Liatris spicata* occurs rarely in Wisconsin but is similar taxonomically to *Liatris pycnostachya*, which is not found in Ontario. The two species have a very similar ecological response along the gradient (Figures 1f and 4f).

There are some notable differences in species response between the two regions in the drier stands, where *Panicum oligosanthes* and *Elymus canadensis* have higher presence values in Ontario's dry stands (Figures 1a and 4a) and *Liatris aspera* and *Koeleria macrantha* have higher values in the dry-mesic (Figures 1c and 4c). The species that differs most between these regions is *Elymus canadensis*. It is most constant in dry prairies of Ontario but is optimal in wet-mesic prairies of Wisconsin.

Ontario dry prairies also differ from those in Wisconsin in terms of physiography. Ontario sites are primarily ancient inland stabilized dune systems and glacial beach shorelines, with some stony slopes, but in Wisconsin dry prairie occurs almost exclusively on inland steep hillsides with thin soil. This in turn affects their species composition. For example, *Elymus canadensis* was seen to differ substantially in species response between Wisconsin and Ontario dry prairies (Figures 1a and 4a). When the response of *Elymus canadensis* in other habitats in Wisconsin was examined, its highest presence values was in dry lake dune sites (Curtis 1959). If this presence value is plotted in the dry prairie segment then we obtain a response comparable to that in Ontario (Figures 1a and 4a with dotted line). Similar trends were observed for *Equisetum hyemale*, *Poa compressa*, and *Oenothera biennis*. Further comparisons of floristic lists of other vegetation types between regions will allow us to test the importance of the trends observed here. In so doing we may gain greater insight into the different regional processes controlling vegetation patterns.

CONCLUSION

In conclusion, prairies in southern Ontario are favoured by a unique combination of moisture, sandy and stony substrates, and frequent fires. Many sites show a striking resemblance to prairie sites farther west in the prairie-forest border and have persisted in the region for many hundreds of years. Drier sites on inland stabilized sand dunes and glacial beach shorelines continue to support a number of prairie and prairie-like communities, but have a variable composition that is less related to drier prairies farther west. These areas show high resemblance to sand prairies and oak savanna. Together these prairies and associated communities comprise a distinctive grassland vegetation type within southern Ontario's deciduous forest region.

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Appendix 1. List of prevalent species for the five moisture segments of Ontario prairie. Species are arranged alphabetically with their % presence within a segment. Absence of a value indicates the species was not prevalent in the segment, but it may have been present at some lower value.

	Moisture Segment (No. of Stands)				
Species	Dry (19)	Dry-mesic (10)	Mesic (9)	Wet-mesic (19)	Wet (6)
Achillea millefolium		60	67		
Agropyron repens	68				
Agrostis gigantea		70	100	68	50
Andropogon gerardii	89	90	89	89	50
Andropogon scoparius	95	90	67	47	
Anemone cylindrica	74	70	67		
Anemone virginiana		40			
Antennaria neglecta	42	70	67		
Antennaria plantaginifolia	42				
Apios americana		40	44	63	
Apocynum androsaemifolium	47				
Apocynum cannabinum		40	89	84	100
Arenaria stricta	42				
Aristida purpurascens			44		
Asclepias incarnata					50
Asclepias sullivantii			44		50
Asclepias syriaca	53				
Asclepias tuberosa	63	40	56		
Asparagus officinale			56		
Aster azureus	68	90	89	58	
Aster dumosus				42	
Aster ericoides	42	80	100	84	67
Aster laevis	37	40	56		
Aster novae-angliae		50	78	84	100
Aster sagittifolius	30				
Aster simplex			56	58	100
Aster umbellatus					34
Calamagrostis canadensis		30	67	95	100
Carex bicknellii				37	
Carex buxbaumii				37	100
Carex conoidea					50
Carex granularis				37	
Carex lanuginosa			44	58	83
Carex muhlenbergii	32				
Carex pensylvanica	42	80	78		
Carex sartwellii					67
Carex stricta					67
Ceanothus americanus	37				
Cerastium vulgatum		40			
Chrysanthemum leucanthemum		40			
Cicuta maculata				42	
Cirsium arvense					50

Appendix 1, continued.

Cirsium discolor		40	67	42	83
Comandra richardsiana	47	50	56	53	
Convolvulus sepium			56	37	83
Coreopsis tripteris			56		
Cornus obliqua					50
Cornus racemosa	37	80	89	74	83
Corylus americanus			44		
Cyperus filiculmis	42				
Danthonia spicata	37	50			
Daucus carota	58	60	56		50
Desmodium canadense	47	80	100	89	67
Dryopteris palustris				63	83
Eleocharis elliptica			44	58	83
Elymus canadensis	37				
Equisetum arvense	37	50	78	84	
Equisetum hyemale	42	40	67		
Erigeron canadensis	32				
Erigeron philadelphicus				37	
Erigeron strigosus		50	56		
Eupatorium maculatum					50
Euphorbia corollata	37	40	44		
Fragaria virginiana	58	100	89	84	67
Galium boreale	42				
Galium palustre					50
Geranium maculatum		40			
Gerardia purpurea			44	37	67
Gerardia tenuifolia				37	
Helenium autumnale			44	58	100
Helianthemum canadense	32				
Helianthus giganteus				68	100
Hieracium florentinum	42	40			
Hypericum perforatum	63	50			
Hypoxis hirsuta			44	63	83
Iris versicolor				37	100
Juncus balticus		30	33	53	
Juncus dudleyi				37	
Juncus greenei			56		
Juncus tenuis			67		
Juncus torreyi				58	
Krigia biflora				37	
Lathyrus palustris			44	74	100
Lechea intermedia	32				
Lespedeza capitata	68	70	78		
Liatris aspera		40			
Liatris cylindracea	47				
Liatris spicata		40	89	74	50
Linaria vulgaris	37	40			
Lithospermum canescens		40			
Lobelia spicata			67	47	
Luzula multiflora			44		
Lycopus americanus			56	63	83

Appendix 1, continued.

Lycopus uniflorus				42	83
Lysimachia quadriflora			56	68	83
Lythrum alatum					67
Melilotus alba	63	60	33		
Mentha arvensis					50
Monarda fistulosa	63	100	100	79	34
Muhlenbergia mexicana			56	42	
Oenothera biennis	58	50		42	
Onoclea sensibilis				37	
Panicum boreale					34
Panicum lan. var implicatum		50	33	47	34
Panicum oligosanthes	42				
Panicum sphaerocarpon			44		
Panicum virgatum		30	100	79	67
Pedicularis lanceolata				37	
Plantago lanceolata		30			
Poa compressa	84	90	78		
Poa pratensis	84	80	89	68	67
Polygala sanguinea		40			
Polygonum coccineum					67
Populus deltoides (sdlgs)			44		
Potentilla recta	47	30			
Potentilla simplex	32		44		34
Prenanthes racemosa				53	
Prunella vulgaris		60	67		
Prunus virginiana	47	40			
Pteridium aquilinum	37				
Pycnanthemum virginianum		40	89	84	83
Pyrus malus (sdlgs)		40			
Quercus palustris (sdlgs)				42	
Quercus velutina (sdlgs)	58	40			
Rhus aromatica	47				
Rhus glabra			56		
Rhus radicans	58				
Rhus typhina	74	40			
Rosa blanda					67
Rubus flagellaris					34
Rudbeckia serotina		80	100	89	83
Rumex acetosella	47				
Salix discolor				37	
Salix humilis		60	56	37	
Scleria triglomerata			67		
Senecio aureus				42	34
Solidago altissima		50	67	42	34
Solidago canadensis	63	80	78	68	100
Solidago gigantea			56	68	34
Solidago graminifolia		60	100	74	100
Solidago juncea	74	90	56	37	50
Solidago nemoralis	84	100	67		
Solidago ohioensis					34
Solidago riddellii			44	37	

Appendix 1, continued.

Solidago rigida		40	78	53	
Sorghastrum nutans	53	80	78	74	67
Spartina pectinata			56	74	100
Spirea alba					50
Sporobolus asper			33		
Sporobolus cryptandrus	37				
Taraxacum officinale		30			
Thalictrum polygamum				42	
Tragopogon pratensis	53				
Verbascum thapsus	58				
Vernonia altissima			78	79	83
Veronica officinalis		30			
Veronicastrum virginicum		40	89	79	50
Viola papilionacea			33	47	50
Vitis riparia	68	70	89	84	50
Zizea aurea			33	42	
No. of prevalents (= avg. no. of species per stand)	59	68	79	72	63
Total species	212	234	205	238	147
No. of stands	19	10	9	19	6

STONE ROAD ALVAR, PELEE ISLAND: MANAGEMENT OF AN UNUSUAL OAK SAVANNAH COMMUNITY TYPE IN THE WESTERN LAKE ERIE ARCHIPELAGO

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Abstract. Stone Road Alvar is the southernmost alvar in Canada, supporting a rare savannah ecosystem with an exceptionally diverse flora. Several species found here are at or near their northern distribution and occur in few, if any, other locations in Canada. Development threats prompted the Federation of Ontario Naturalists (FON) to acquire 42 ha (106 acres) of the alvar in 1984 and include it in their province-wide nature reserve system. Two adjacent properties were later acquired by the Essex Region Conservation Authority (ERCA). Management for perpetuation and enhancement of the savannah/alvar habitat is proving to be a major challenge. The logistical difficulties associated with an island location add to management costs. In addition the site has few natural fire-breaks and is habitat to two provincially endangered species. The ecosystem appears to be driven by extreme edaphic conditions (i.e. cyclical periods of severe drought) and fire. Inventories and quantitative sampling of representative communities were carried out jointly by the FON, ERCA and Ontario Ministry of Natural Resources (OMNR) to investigate the natural features and dynamics of the alvar and savannah for the purpose of future habitat management.

INTRODUCTION

Stone Road Alvar is located on Pelee Island, the largest of the twenty-one islands that constitute the Lake Erie archipelago.The island is within the County of Essex, Ontario (41° 45' N, 76° 05'E) and represents the most southerly inhabited land mass in Canada. The 4,000 ha (10,630 acres) island supports approximately 230 permanent residents (Wilkens and Waldron, 1988). Most of the island is devoted to agriculture, mainly soybeans and corn. More recently the island has re-established its wine growing heritage and provides all the vineyards for Pelee Island Wines of Kingsville. Limestone quarrying, commercial fishing and tourism are three additional industries based on the island.

The entire alvar site lies on the southeast corner of the island, consisting of Lots 41,42,43 and Part Lots 37 and 38. A site location and property boundaries maps is illustrated in Figure 1.

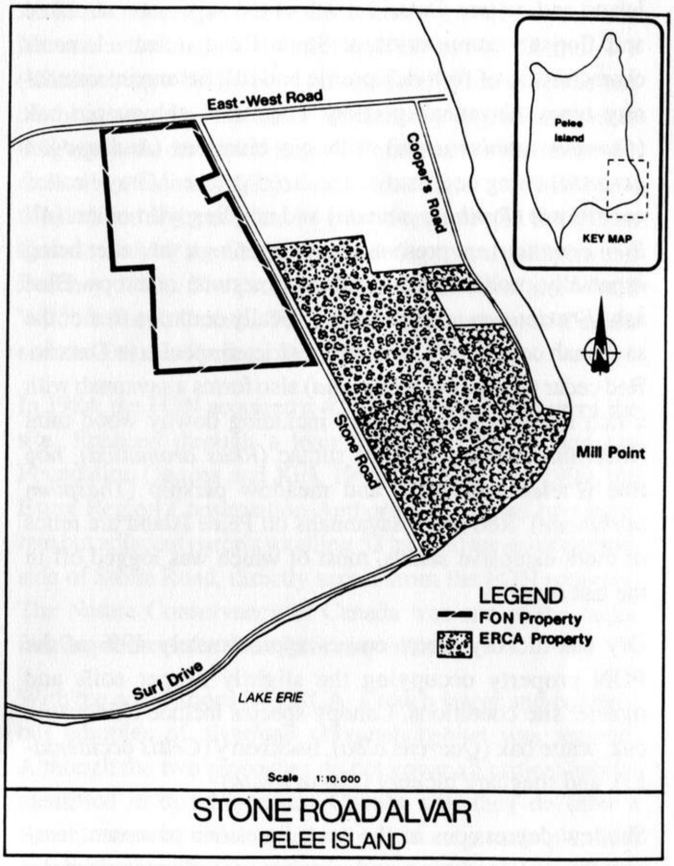

Figure 1. Site location and property boundaries.

Pelee Island was originally a series of five limestone outcrops loosely connected by sand barrier beaches and marsh. The island was once covered by a post-glacial lake 6,000 years ago, which laid down a layer of thin, silty sediments over the limestone bedrock. The limestone and dolomite bedrock are Upper Silurian and Lower Devonian in age and are very rich in fossils, including crinoids, brachiopods, corals, snails and trilobites (Richards et al. 1949).

The silt and clay sediments that have been accumulating since the glacier's retreat have formed the shallow soils of Stone Road Alvar. The soils over the site consist entirely of Farmington loam. This loam is characterized by variable texture underlain by limestone bedrock at depths of one metre or less (Richards et al. 1949). Moisture conditions are highly variable especially where the overburden is shallow (i.e. less than 0.5 m). In spring the soils often become saturated and internal drainage is restricted due to the underlying bedrock. Conversely in mid-to-late summer the overburden dries out, often creating extreme drought conditions. The soils are relatively alkaline; samples taken over the course of field work had pH values ranging from 7.1 to 7.7. Due to their shallowness the soils lack a distinct profile and consist almost entirely of fibric and organic mineral horizons.

In an ordination and classification analysis of selected alvars in Ontario, Stone Road alvar had the highest overall biomass and soil depth (Belcher et al. 1992). Unlike the rock barrens and grassy meadows of alvar sites found on Manitoulin Island and eastern Ontario much of the vegetation structure and floristic composition at Stone Road reflect elements characteristic of forb rich prairie and oak savannah community types. Savannah portions consist of chinquapin oak (*Quercus muhlenbergii*) with big bluestem (*Andropogon gerardii*) being confined to localized patches. Gray-headed coneflower (*Ratibida pinnata*) and nodding wild onion (*Allium cernuum*) are present in most openings, the latter being especially prolific around barren limestone outcrops. Blue ash (*Fraxinus quadrangulata*), a locally common tree of the savannah community, is a very restricted species in Ontario. Red cedar (*Juniperus virginiana*) also forms a savannah with a rich herbaceous understory including downy wood mint (*Blephilia ciliata*), fragrant sumac (*Rhus aromatica*), hop tree (*Ptelea trifoliata*), and meadow parsnip (*Thaspium barbinode*). Red cedar savannahs on Pelee Island are relics of more extensive stands, most of which was logged off in the last century.

Dry oak-hickory forest covers approximately 40% of the FON property occupying the slightly deeper soils and moister site conditions. Canopy species include chinquapin oak, white oak (*Quercus alba*), hackberry (*Celtis occidentalis*), and shagbark hickory (*Carya ovata*).

Shallow depressions in the open limestone pavement, seasonally wet in spring and autumn, are characterized by mosses, algae, sedges and spike rushes. These are very ephemeral communities which can become dormant during a dry spell. Dry limestone outcrops are niches for specialized plants such as corn salad (*Valerianella umbilicata*), false pennyroyal (*Isanthus brachiatus*), conobea (*Leucospora multifida*), narrow-leaved vervain (*Verbena simplex*), and great plains ladies'-tresses (*Spiranthes magnicamporum*) plus a number of rare graminoids.

Extremes in moisture are most apparent on limestone pavement. Moisture conditions may vary tremendously from year to year. During the summers of 1988 and 1991 drought stress was so severe that complete browning and defoliation of both shrub and open grown savannah trees occurred by late July. This does not appear to cause mortality among the well established chinquapin oak, however there was considerable dieback in dogwood (*Cornus drummondii*), prickly ash (*Xanthoxylum americanum*) and to a lesser extent fragrant sumac. Even in drought years the moisture returns in the fall so that for approximately half the year the alvar experiences moist to saturated conditions.

The 55 native "alvar" species at this site make the Stone Road site one of the most unusual alvars in Ontario (Catling et al. 1975, Belcher et al. 1992). In the 1970s several new plants discovered on the alvar were additions to the flora of Canada (Duncan 1973, Campbell and Reznicek 1977). Four species of plants (*Blephilia ciliata, Muhlenbergia sobolifera, Solidago ulmifolia, Triosteum angustifolium*) are not currently known elsewhere in Canada (M.J. Oldham, pers. comm. 1993). In 1983, 14 species were unknown elsewhere in Essex County and 19 species occurred nowhere else in the Erie Islands archipelago (Oldham 1983). To date 48 provincially rare and 33 regionally rare plant species have been recorded for this site. From a faunal perspective the alvar is habitat to the provincially endangered blue racer (*Coluber constrictor foxi*) and the Lake Erie water snake (*Nerodia sipedon insularum*). Breeding birds rare to Ontario and Canada include yellow-breasted chat (*Icteria virens*), white-eyed vireo (*Vireo griseus*) and acadian flycatcher (*Empidonax virescens*). Two butterflies very rare in Canada include the giant swallowtail (*Papilio cresphontes*) and tawny emperor (*Asterocampa clyton*).

Table 1 is a listing of provincially rare plants found at Stone Road Alvar, based on rarity determined by the Canadian Museum of Nature (Argus et al. 1982-1987). Two species (*Muhlenbergia sobolifera* and *Crataegus dilitata*) are most likely provincially rare but were discovered since the publication of the ***Atlas of Rare Vascular Plants of Ontario*** (Oldham, personal communication 1993).

Table 1. Provincially rare plants of Stone Road Alvar.

(as designated by Argus et al. 1982- 1987)

1)	*Allium cernuum*	Nodding Wild Onion
2)	*Asclepias purpurascens*	Purple Milkweed
3)	*Asclepias verticillata*	Whorled Milkweed
4)	*Aster shortii*	Short's Aster
5)	*Blephilia ciliata*	Downy Wood Mint
6)	*Camassia scilloides*	Wild Hyacinth
7)	*Campsis radicans*	Trumpet Creeper
8)	*Carex davisii*	Sedge
9)	*Carex gracilescens*	Sedge
10)	*Carex jamesii*	Sedge
11)	*Carex leavenworthii*	Sedge
12)	*Carex meadii*	Sedge
13)	*Carex muskingumensis*	Sedge
14)	*Carex oligocarpa*	Sedge
15)	*Carya lacinosa*	Big Shellbark Hickory
16)	*Cerastium velutinum*	Large Mouse-eared Chickweed
17)	*Chaerophyllum procumbens*	Creeping Chervil
18)	*Chenopodium standleyanum*	Standley's Goosefoot
19)	*Cornus drummondii*	Rough-leaved Dogwood

Table 1, continued.

20)	*Corydalis flavula*	Yellow Corydalis
21)	*Crataegus dissona*	Hawthorn
22)	*Crataegus mollis var. gigantea*	Hawthorn
23)	*Euonymus atropurpureus*	Burning Bush
24)	*Euphorbia obtusata*	Blunt-leaved Spurge
25)	*Fraxinus quadrangulata*	Blue Ash
26)	*Geum vernum*	Spring Avens
27)	*Gleditsia triancanthos*	Honey Locust
28)	*Heuchera americana*	Alum Root
29)	*Lactuca floridana*	Wild Blue Lettuce
30)	*Leucospora multifida*	Conobea
31)	*Lythrum alatum*	Winged Loosestrife
32)	*Morus rubra*	Red Mulberry
33)	*Myosotis macrosperma*	Scorpion Grass
34)	*Panicum gattingeri*	Gattinger's Panic Grass
35)	*Phacelia purshii*	Miami Mist
36)	*Polygonum erectum*	Erect Knotweed
37)	*Ptelea trifoliata*	Hop Tree
38)	*Ratibida pinnata*	Gray-headed Coneflower
39)	*Rosa setigera*	Prairie Rose
40)	*Solidago ulmifolia*	Elm-leaved Goldenrod
41)	*Spiranthes magnicamporum*	Great Plains Ladies' Tresses
42)	*Spiranthes ovalis*	Oval Ladies' Tresses
43)	*Strophostyles helvola*	Wild Bean
44)	*Thaspium barbinode*	Hairy-jointed Meadow Parsnip
45)	*Thaspium trifoliatum*	Meadow Parsnip
46)	*Triosteum angustifolium*	Yellow Horse Gentian
47)	*Valerianella umbilicata*	Corn-salad
48)	*Viola rafinesquii*	Rafinesque's Violet

Various forms of disturbance have occurred in the Stone Road area that have influenced the site features. One major form of disturbance has been agricultural activities. The area east of Stone Road was grazed until approximately the early 1970s and there is also evidence of former cultivation. Fire too, occurred periodically throughout the area and would have played a role in sustaining the alvar vegetation communities. In recent years the lack of fire and grazing has most likely contributed to the advanced succession that has now taken place on both properties. Logging was also conducted in past years exploiting the valuable red cedar timber that at one time formed extensive stands in and around the alvar. These activities, or lack of, have resulted in major changes throughout parts of the site, altering the vegetation structure of the alvar/oak savannah complex.

Past grazing has probably contributed to the predominance of cool season grasses (*Poa compressa, P. pratensis*) in all shrub, alvar and savannah communities. Aggressive species now invading the open habitats include red ash (*Fraxinus pennsylvanica*), prickly ash, hawthorns (*Crataegus spp.*), dogwoods (*Cornus racemosa, C. drummondii*), sumacs (*Rhus aromatica, R. typhina*) and dog rose (*Rosa canina*).

RESEARCH

Background

A preliminary life science report was prepared by the Ontario Ministry of Natural Resources (OMNR) in 1977 which included the mapping of vegetation communities within the core alvar area (OMNR, 1977). Subsequently Stone Road Alvar was identified by the OMNR as a life science Area of Natural and Scientific Interest (ANSI) in Site District 7-1 (Klinkenberg 1984). The alvar was further identified as one of the most significant Environmentally Significant Areas (ESA) within the Essex Region Conservation Authority jurisdiction (Oldham 1983). Stone Road Alvar was also identified as one of the original 36 critical unprotected Carolinian Canada sites by the Carolinian Canada program (Eagles and Beechey 1985). The program is a joint effort of the World Wildlife Fund, Canada, The Nature Conservancy of Canada and the Ontario Heritage Foundation.

In 1984, the FON acquired a 42 ha (106 acre) portion of the site, financed through a loan from the Ontario Heritage Foundation (Jaques and Kirk 1985). In 1987 and 1990, the Essex Region Conservation Authority purchased two separate but adjacent parcels totalling 53 ha (130 acres) of the east side of Stone Road, directly across from the FON property. The Nature Conservancy of Canada was one of the major funding sources for these later acquisitions.

With the acquisitions by ERCA, a much larger and contiguous complex of alvar/oak savannah habitat was secured. Although the two properties do not cover all critical habitat identified in this Carolinian Canada site, they do offer a sizeable unit in which to develop a management plan and engage in management activities to perpetuate early successional stages over significant portions.

From the outset, it was realized by all agencies that perpetuation of the oak savannah communities on the nature reserve would require considerable effort in terms of preparatory field investigations and actual hands-on management. Concerns over applying direct management prescriptions or designing trail access through the property before obtaining a better understanding of key vegetation communities, community age structure, soils, species inventories, and rare species locations prompted the FON in conjunction with the OMNR and ERCA to initiate an ecological investigation.

The goal of the investigation was to conduct ecological research on the natural features and dynamics of an alvar and oak savannah ecosystem at the Stone Road alvar complex for the purpose of planning and management. Specifically the objectives were:

Table 2. Plot #7 (ERCA property).

Species	%F	%C	%RF	%RC	IV
Poa compressa	100	90	15.15	45.45	30.30
Poa pratensis	85	15.5	12.87	7.828	10.35
Rubus occidentalis	75	15	12.12	7.575	9.848
Cornus drummondii	75	7.5	11.36	3.787	7.575
Rhus typhina	45	10.5	6.818	5.303	6.06
Solidago sp.	50	9	7.575	4.545	6.06
Rubus allegheniensis	30	5	4.545	2.525	3.535
Fragaria virginiana	30	5	4.545	2.525	3.535
Parthenocissus inserta	30	4	4.545	2.02	3.282
Rhus glabra	15	4.5	2.272	2.272	2.272
Hypericum sp.	20	2	3.03	1.01	2.01
Ratibida pinnata	20	2	3.03	1.01	2.01
Monarda fistulosa	15	1.5	2.272	0.757	1.515
Crataegus sp.	10	1	1.515	0.505	1.01
Hypericum perforatum	10	1	1.515	0.505	1.01
Viburnum lentago	10	1	1.515	0.505	1.01
Carex molesta	5	0.5	0.757	0.252	0.505
Commandra umbellata	5	0.5	0.757	0.252	0.505
Daucus carota	5	0.5	0.757	0.252	0.505
Geum sp.	5	0.5	0.757	0.252	0.505
Hypericum perforatum	5	0.5	0.757	0.252	0.505
Lepidium campestre	5	0.5	0.757	0.252	0.505
Nepeta cataria	5	0.5	0.757	0.252	0.505
Rhus typhina	5	0.5	0.757	0.252	0.505

- To conduct vegetation sampling and tree coring to establish base line information for future monitoring studies before and after management activities are implemented.

- To refine on-site resource data through inventories, and community and rare species mapping.

- To investigate a means of habitat management through lead agencies which would ensure the perpetuation of alvar and oak savannah communities and which would reverse successional patterns over certain portions of the site.

- To develop a system of management units for the area which would recognize critical zones. The system would be based on resource inventory data and the protection of critical life science elements.

METHODS

The quantitative method for vegetation sampling used in this project was modified from a sampling technique that had been used at the Ojibway Prairie Provincial Nature Reserve (Pratt, 1979). The vegetation of the Ojibway Prairie has many structural similarities to Stone Road alvar.

Eight 15x30 metre plots were set up and sampled from May to August, 1988, on FON and ERCA properties. The location of each plot was chosen to represent the range of vegetation communities on both the FON and ERCA properties. Within each plot, 20 quadrats (1m x 1m) were randomly established. This particular quantitative sampling method is standard for assessing non-forested vegetation communities (Smith 1974).

Within each square metre quadrat, cover estimates and frequency values were recorded for each plant species. Cover estimates included any vegetation matter within the vertical boundaries of the quadrat. Trailing vines or overhanging branches of saplings and shrubs were also included in the results if they were within the quadrat boundaries. Plant cover was measured using five general cover class values. This simplified the procedure and saved considerable time. Using cover classes also helped reduce the amount of error inherent in obtaining visual estimates.

A total of 26 cores were extracted for trees representative of various habitats. Species cored included chinquapin oak, white oak, bur oak, blue ash, red ash, and red cedar. Core samples were analyzed at the Ecology Lab, Faculty of Environmental Studies, University of Waterloo, Ontario. Using a

Table 3. Plot #3 (FON property).

Species	%F	%C	%RF	%RC	IV
Poa compressa	100	90	10.07	36.99	23.53
Fragaria virginiana	100	19	10.07	7.809	8.939
Allium cernuum	100	17	10.07	6.987	8.528
Ratibida pinnata	75	13.5	7.552	5.548	6.550
Commandra umbellata	50	15	5.035	6.165	5.600
Carex granularis	60	12	6.042	4.932	5.487
Poa pratensis	70	9	7.049	3.699	5.374
Senecio pauperculus	70	8	7.049	3.288	5.168
Rosa blanda	40	7	4.028	2.877	3.452
Cornus racemosa	25	10.5	2.517	4.315	3.416
Carex meadii	40	4	4.028	1.644	2.836
Eleocharis sp.	35	3.5	3.524	1.438	2.481
Elymus villosus	25	5.5	2.517	2.260	2.389
Xanthoxylum americanum	25	5.5	2.517	2.260	2.389
Blephilia ciliata	25	3.5	2.517	1.438	1.987
Juncus biflorus	20	3	2.014	1.233	1.623
Cornus drummondii	15	2.5	1.510	1.027	1.269
Scutellaria parvula	15	1.5	1.510	0.616	1.063
Carex molesta	15	1.5	1.510	0.616	1.063
Cerastium velutinum	10	2	1.007	0.882	0.914
Viburnum rafinesquianum	10	2	1.007	0.882	0.914
Apocynum androsaemifolium	10	1	1.007	0.441	0.709
Hypericum perforatum	10	1	1.007	0.441	0.709
Parthenocissus inserta	5	1.5	0.503	0.616	0.560
Heuchera americana	5	0.5	0.503	0.205	0.354
Monarda fistulosa	5	0.5	0.503	0.205	0.354
Quercus muehlenbergii	5	0.5	0.503	0.205	0.354
Rhus aromatica	5	0.5	0.503	0.205	0.354
Rosa canina	5	0.5	0.503	0.205	0.354
Carex davisii	5	0.5	0.503	0.205	0.354
Asclepias purpureum	1	0.1	0.100	0.041	0.070
Potentilla recta	1	0.1	0.100	0.041	0.070
Lotus corniculata	1	0.1	0.100	0.041	0.070
Rumex orbiculata	1	0.1	0.100	0.041	0.070
Smilacina stellata	1	0.1	0.100	0.041	0.070
Solidago sp.	1	0.1	0.100	0.041	0.070
Zigadenus glaucus	1	0.1	0.100	0.041	0.070
Fraxinus americana	1	0.1	0.100	0.041	0.070
Rhus radicans	1	0.1	0.100	0.041	0.070
Ulmus americana	1	0.1	0.100	0.041	0.070
Viburnum lentago	1	0.1	0.100	0.041	0.070
Vitis riparia	1	0.1	0.100	0.041	0.070
Agrosits gigantea	1	0.1	0.100	0.041	0.070

specially calibrated instrument, annual increment growth was measured under a low power microscope. All data were entered into a specialized software package designed by Dr. R. Suffling (Faculty of Environmental Studies). From the data it was possible to generate histograms depicting growth rates for a given time period (Figures 2, 3, 4, 5).

The OMNR made a significant contribution to the ecological survey through a qualitative inventory resulting in a collection of floristic and vegetation community data for the entire alvar area. These additional data have provided invaluable information, complementing the results obtained from the quadrats and tree cores.

RESULTS

Plot Sampling

A sample of the plot data provides a base line from which to monitor vegetation changes over time, particularly after a prescribed burn (Tables 2,3,4). The species composition, richness and frequency within each large plot illustrates variability based on degree of succession, soil depth and presence of limestone outcrops. In all cases the Importance Value of *Poa compressa* greatly exceeded all other species with nearly 100% frequency of all quadrats sampled.

These data indicate that at this time the ERCA property is characterized by a higher proportion of woody material and as well as containing a generally lower floristic diversity than the FON property. The larger amount of woody material would, of course, reflect the more advanced stage of succession on the ERCA property.

It was not the purpose of this sampling exercise to derive a classification analysis of the vegetation within the alvar or to examine species relationships or the ecological relationships between species composition and measured variables. The emphasis was on the protection measures that are required to maintain this important ecosystem.

Randomness was not used in plot selection, instead a good cross section of habitats in need of management were chosen. In all but one case open alvar and savannah communities were chosen as they represented the type of habitat that requires the most ecosystem management. The ERCA plots showed a difference in structure and floristics from all FON plots reflecting differences in the land use history of the two properties. These differences are central to developing management recommendations.

Tree Cores

It was evident from the core data that species like chinquapin oak are surviving under very stressed conditions (Figure 2).

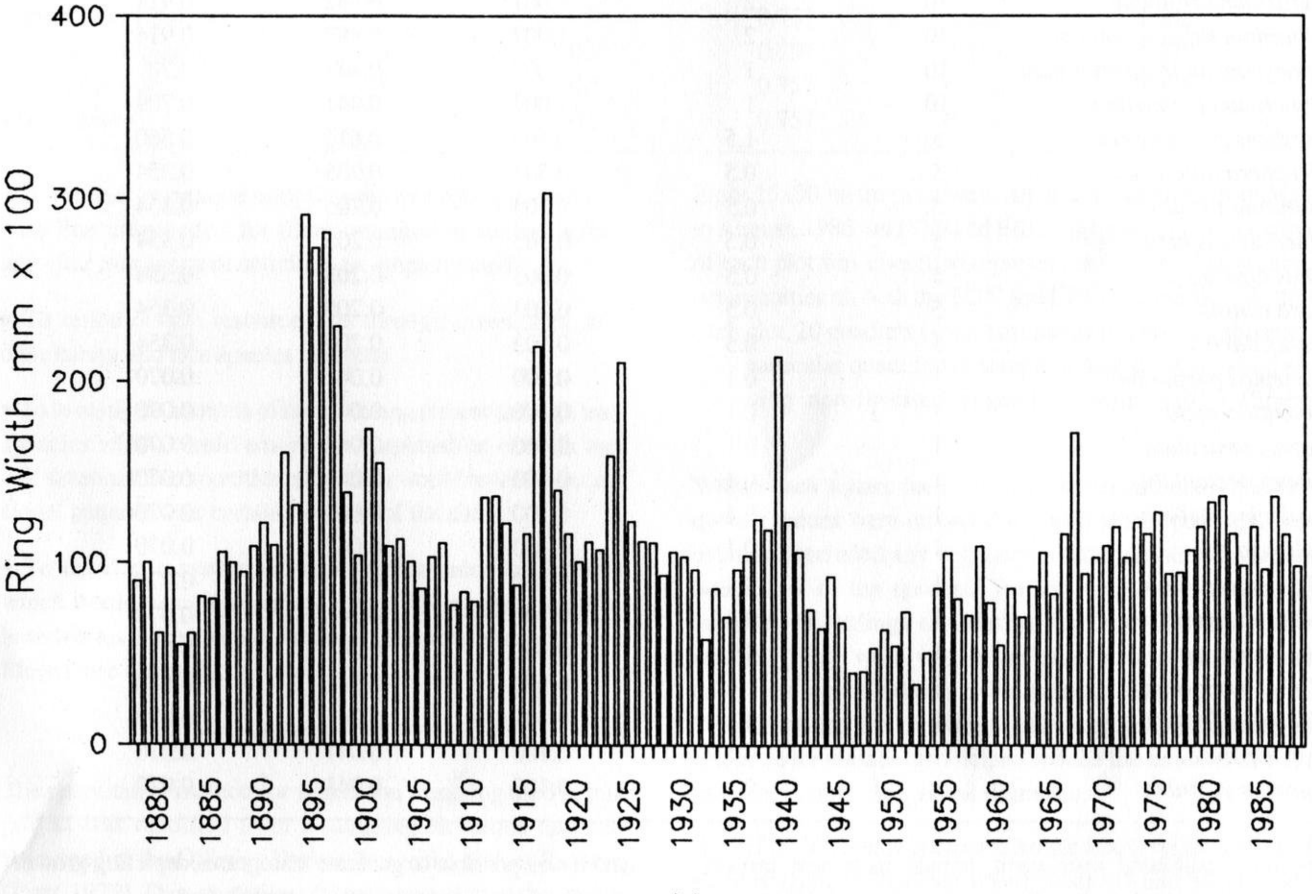

Figure 2. Chinquapin Oak (Plot #5, Core #12).

Table 4. Plot #4 (FON property).

Species	%F	%C	%RF	%RC	IV
Poa compressa	95	70.5	15.96	36.43	26.2
Allium cernnum	90	38	15.12	19.63	17.38
Poa pratensis	65	21.5	10.92	11.11	11.01
Cornus drummondii	45	11.5	7.563	5.943	6.753
Fragaria virginiana	45	7.5	7.563	3.875	5.719
Panicum flexile	30	9	5.042	4.651	4.846
Carex molesta	30	7	5.042	3.617	4.329
Eleocharis compressa	30	3	5.042	1.550	3.296
Fraxinus pennsylvanica	20	5	3.361	2.583	2.972
Juncus dudleyi	25	2.5	4.201	1.291	2.746
Leucospora multifida	15	3.5	2.521	1.808	2.164
Rhus aromatica	15	3.5	2.521	1.808	2.164
Isanthus brachiatus	15	1.5	2.521	0.775	1.648
Rumex crispus	10	1	1.680	0.516	1.098
Prunus virginiana	5	2.5	0.840	1.291	1.066
Hypericum perforatum	5	0.5	0.840	0.258	0.549
Hypericum punctatum	5	0.5	0.840	0.258	0.549
Portulaca oleracea	5	0.5	0.840	0.258	0.549
Juncus sp.	5	0.5	0.840	0.258	0.549
Carex divulsa	5	0.5	0.840	0.258	0.549
Carex lanuginosa	5	0.5	0.840	0.258	0.549
Rosa blanda	5	0.5	0.840	0.258	0.549
Vitis riparia	5	0.5	0.840	0.258	0.549
Cornus racemosa	5	0.5	0.840	0.258	0.549
Amelanchier humulis	5	0.5	0.840	0.258	0.549
Cornus stolonifera	5	0.5	0.840	0.258	0.549
Juniperus virginiana	5	0.5	0.840	0.258	0.549

Growth rates are so slow as to be almost negligible. Tree heights averaged 8 to 12 metres for specimens with cores measuring 100 to 110 years. More cores are required for the oaks as they would appear to be the most important long-term indicator species of edaphic and cyclical drought conditions in both savannah and closed canopy communities. Although physically larger, blue ash has in comparison become established relatively recently (Figure 3). A red ash is a very recent invader, especially on seasonally wet depressions (Figure 4). This species would most likely come in after the discontinuation of grazing. Red cedar may prove to be the most important species in unravelling the clues on recent fire history and drought conditions. Figure 5 illustrates the cyclical patterns of drought in red cedar. In addtion drought stress can be detected periodically along the length of the cores from this species.

DISCUSSION

Stone Road Alvar has many of the same management issues as prairie and oak savannah systems, however differences in edaphic conditions create special problems. Based on the data gathered in sampling plots and tree cores, it is possible to raise a set of management concerns about the short term management and long term viability of the oak savannah and alvar complex. These concerns are itemized as follows:

- Canada bluegrass (*Poa compressa*) is the dominant ground cover species throughout the entire open areas and savannah complexes. With the exception of a closed canopy forest plot, Canada bluegrass achieved an Importance Value far exceeding the next most prevalent species in the plots. The density of Canada bluegrass turf is such that native alvar and prairie species find it difficult to compete over extensive portions of the site. A cool season grass such as this would be largely killed off by spring burning. However, it would appear as if there is an insufficient seed source of native grasses and forbs to replace Canada bluegrass if this species is largely eliminated because of controlled burns.

- Many plots have significant numbers of non-native weedy species, eg. dog rose (*Rosa canina*), and birdsfoot trefoil (*Lotus corniculatus*). In addition, weedy species have aggressively invaded open limestone exposures. Purslane (*Portu-*

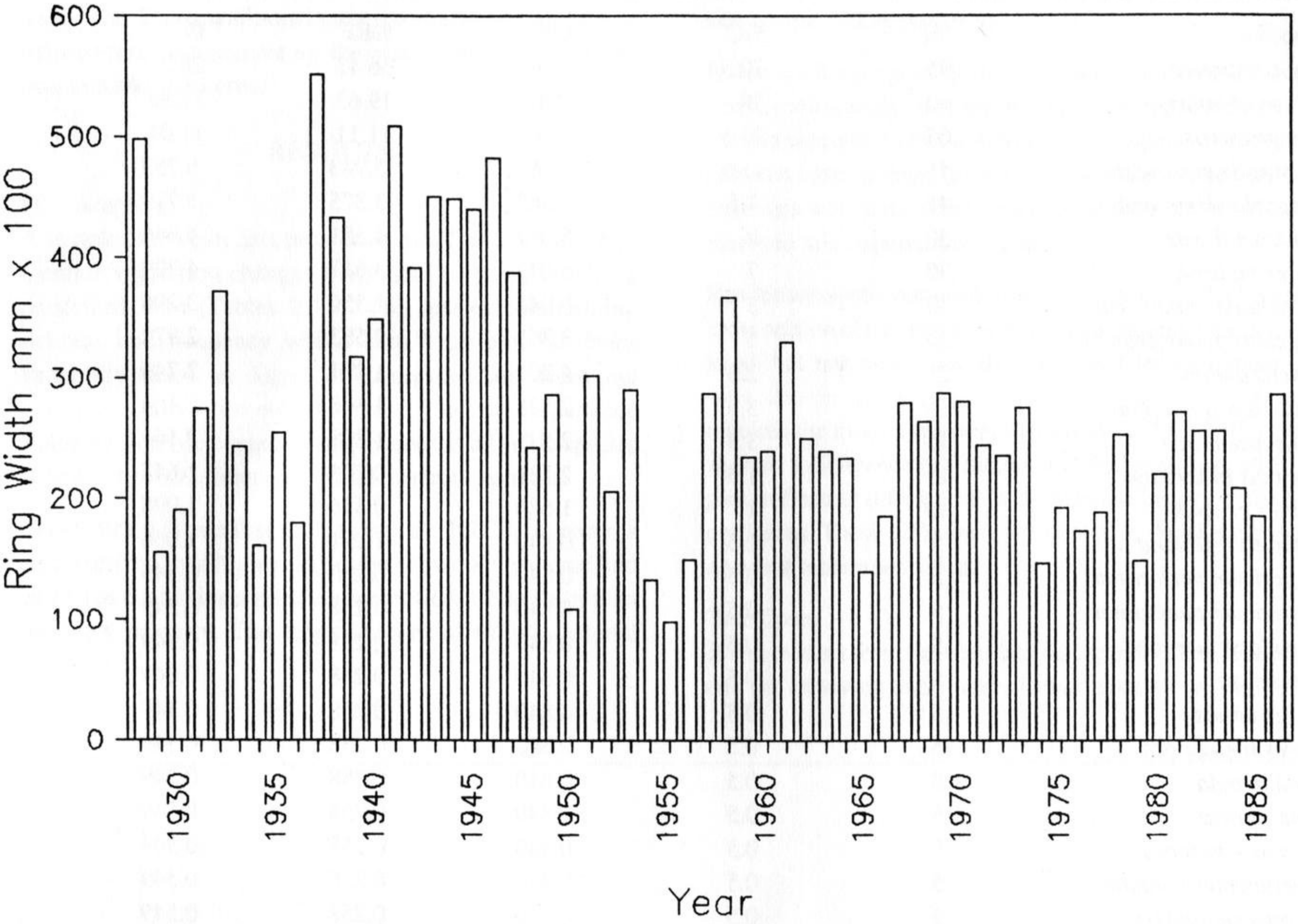

Figure 3. Blue Ash (Plot #1, Core #3).

laca oleracea), and old-witch grass (*Panicum capillare*) occupied most open limestone areas where a number of rare species have established a particular niche.

- Red cedar cores exhibited maximum ages of 35 years. This species is susceptible to intense fire which would indicate that the occurrence of fire has been very limited or absent during this period. The red cedar savannah contains one of the richest floral assemblages of native prairie and alvar species on the property. However, shrub encroachment is filling in the small glades amongst the cedars. The use of fire may curb the shrub growth but destroy the cedars in the process. The site has historically been kept open by grazing as indicated by the numerous old cattle bones scattered in the vicinity. Alternatives to burning may have to be considered for this site until fuel loads have been reduced.

- Red ash is rapidly invading depressions where soils are saturated during part of the year. Following severe drought conditions, this species has shown tremendous resilience by flushing out new shoots once moisture returns. This succession appears to be recent; the oldest trees being some 20-25 years old based on core samples. Large numbers of seedlings and small saplings are now establishing on and around the open limestone glades. These may eventually become a monocultural stand and shade out the specialized flora found here.

- Dense turf mats, primarily of Canada bluegrass, are slowly encroaching over the open limestone. The bare substrate and thin covering of lichens and organic residue is habitat for a number of rare and unusual alvar species. Most cannot tolerate competition.

- Tree cores from good drought indicator species such as red cedar show periods of stress in most years. Drought would appear to be a normal seasonal occurrence. The severity, length and frequency would vary each year. In 1988, drought conditions over southwestern Ontario were probably the most severe in several decades. This was reflected in the defoliation of most open grown trees and shrubs by mid-summer. Stress had been placed on all vegetation during the most critical time, in terms of development, flowering and photosynthesis. An early spring burn followed by a late spring

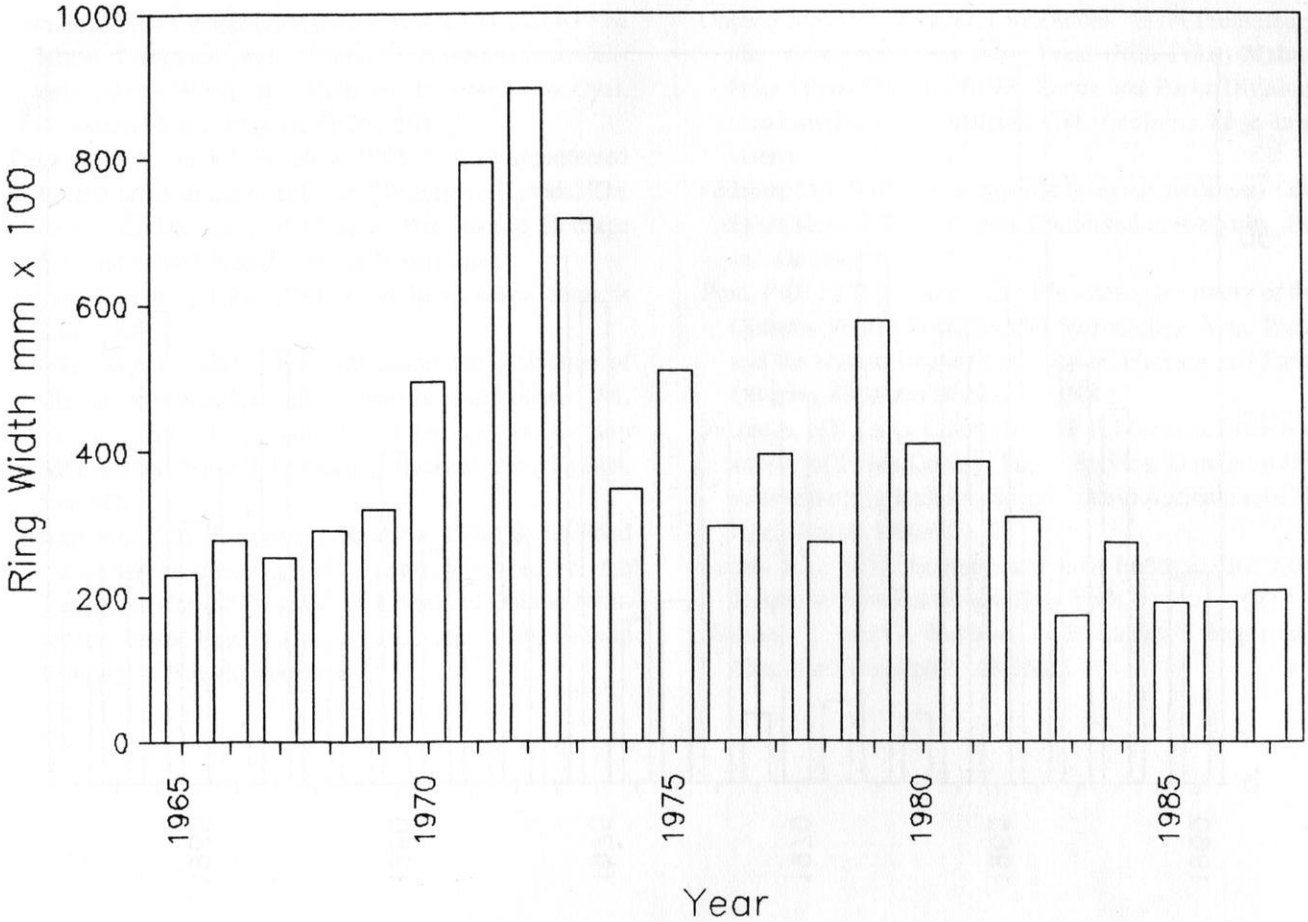

Figure 4. Red Ash (Plot #4, Core #14).

drought may result in more effective control of woody understory. However, it is not known whether the combined effect would be too detrimental to populations of desirable native prairie forbs and allow the invasion of weedy aliens.

- Herbaceous ground cover is not able to recover from trampling during prolonged and intense periods of drought. In 1988, sample plots were heavily trampled and did not recover at all during the entire growing season. This would indicate that the use of the property by large numbers of visitors is not desirable. Unfortunately, a trail system would not alleviate the problem as the openness of the habitat does not confine visitors to a set trail. The problem could be even more acute in areas such as the red cedar savannah where small botanically rich glades are vulnerable to any traffic brought in by a trail system.

- The habitat that is to be restored is a very unusual one. Oldham (1983) reports that Stone Road Alvar is not only unique in Canada but possibly in North America. A combination of factors contribute to the significance of Stone Road Alvar, one of these being that a large number of species are either near the northern or southern range of their natural distribution. It is because of this very significant combination of rare flora and fauna that careful consideration be given to the implementation of management strategies.

- It may not be feasible to consider separate management strategies for each rare species within this alvar complex, therefore special attention must be given to the procedure of a management application. The management of one area or unit at a time will mitigate any potential negative impacts on indigenous fauna by providing unmodified surrounding areas for refuge.

Management Options

Two separate set of management options were recommended for each of the FON and ERCA properties reflecting the differences in successional conditions and ecological diversity between them (Managhan et al. 1990). The property of each agency has been segmented into management units. The application of management application such as a controlled burn would be staged over several years. This would enable each agency to monitor and compare the effectiveness

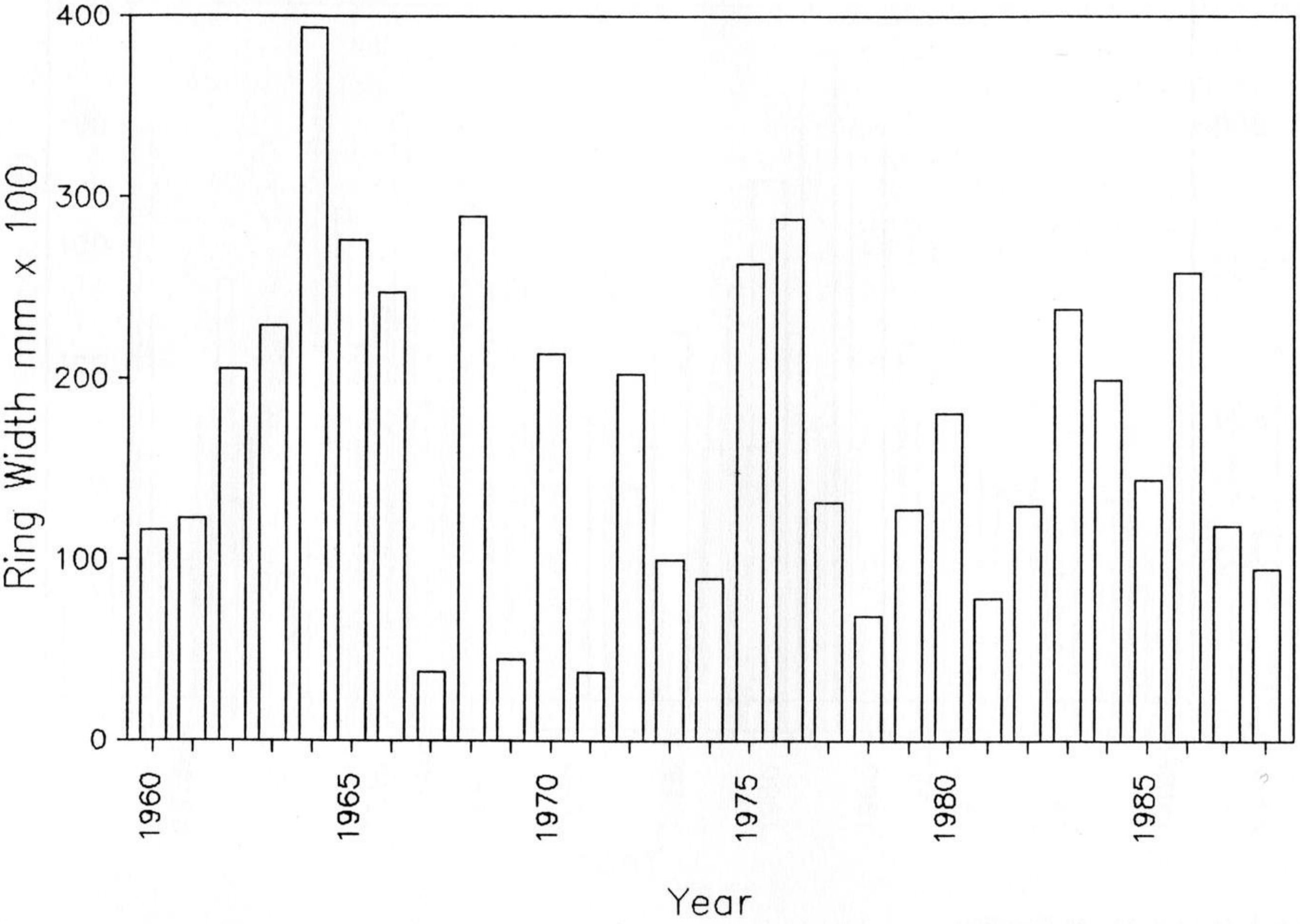

Figure 5. Red Cedar (Plot #5, Core #11.)

of each management technique without posing any major risk to sensitive habitats.

A coordinated effort between ERCA, FON and OMNR is currently underway to undertake a controlled burn on both properties. A major effort will be made to eradicate the tall shrub cover on the ERCA property as a first step toward establishing an early successional environment. A more modest burn is scheduled for the FON property, however it will serve to demonstrate the impact of fire on a variety of high quality alvar and savannah habitats that are contained within the proposed burn area.

ACKNOWLEDGEMENTS

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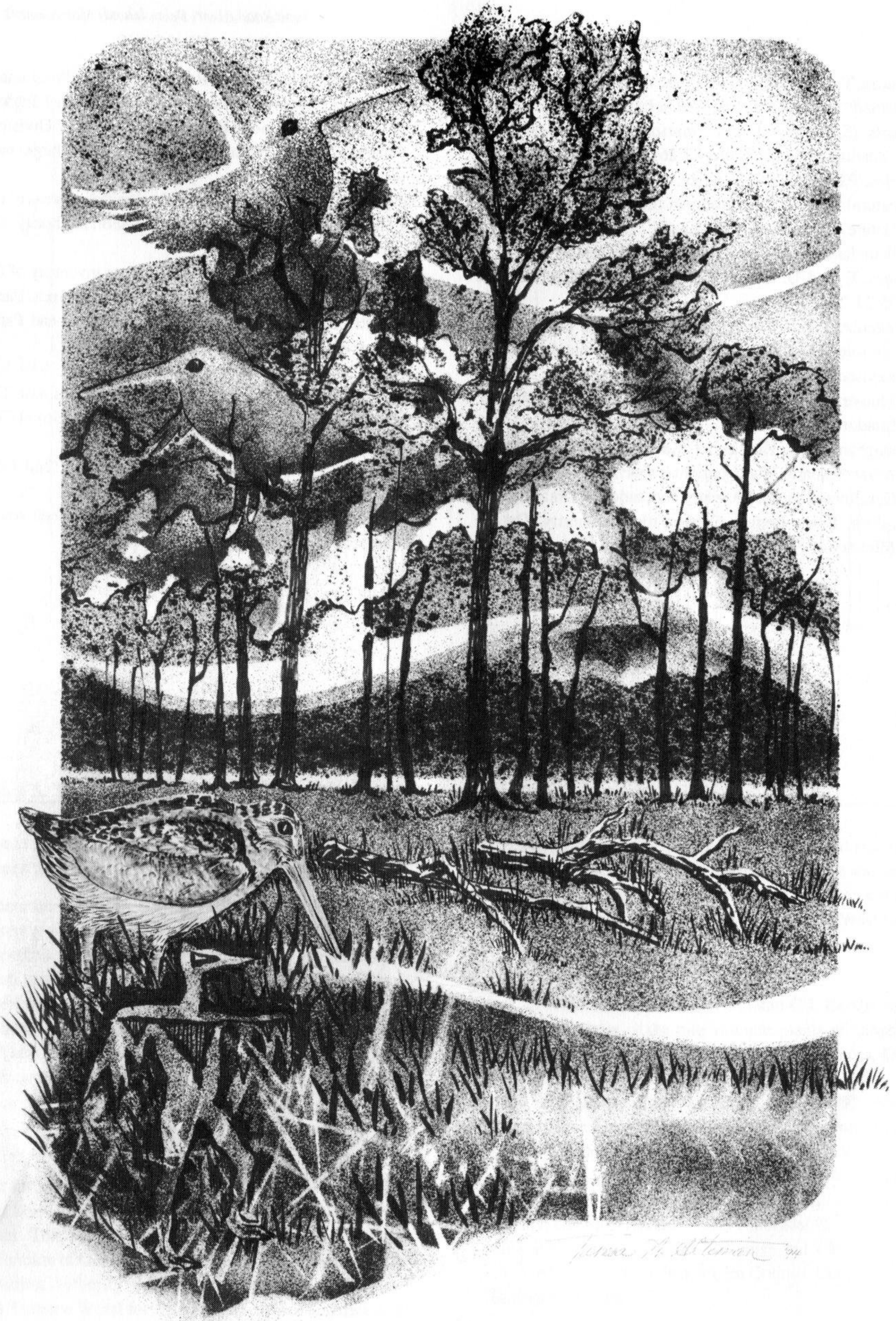

INSECT POLLINATORS OF 12 MILKWEED *(ASCLEPIAS)* SPECIES

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Abstract. More than 1750 insects, collected on 12 species of *Asclepias*, were examined for the number of pollinial sacs extracted from donor flowers and for pollinial attachment to appendage and body hairs. The number of pollinial sacs missing from the translator arms of these pollinia was also determined and presumed to represent the number of pollinial sacs inserted into recipient flowers during pollination. These two figures (the number of pollinial sacs extracted and the number of pollinial sacs inserted) was used to rate the pollinating efficiency of an insect pollinator. The most important pollinators, such as the exotic honey bee (*Apis mellifera*), bumblebees (*Bombus*), large wasps (*Sphex, Tachytes, Myzinum*, and *Polistes*), and large butterflies (*Papilio*), not only carried relatively large numbers of pollinial sacs extracted from donor flowers, but apparently inserted large numbers of pollinial sacs into the stigmatic chambers of recipient flowers. Some milkweeds, such as, *A. hirtella* and *A. viridiflora,* were pollinated by bumblebees, while others, such as, *A. incarnata* and *A. verticillata*, were pollinated by a variety of bees, wasps, and butterflies. It is possible that the colonial mining bee (*Anthophora abrupta*) and other relatively large anthophorid bees (*Ceratina, Epeolus, Florilegus, Melissodes, Peponapis, Tetralonia, Triepoeolus,* and *Xenoglossa*), may have been the major pollinators of many milkweed species in pre-settlement times, but today have been replaced by the exotic honey bee (*Apis mellifera*).

INTRODUCTION

It has been two-hundred years since Sprengel (1793) suggested that insects were important in the removal of pollinia from flowers of *Asclepias.* Brown (1831) was the first to discover how pollination was accomplished in *Asclepias* and to conclude that insect vectors were absolutely necessary in the pollination of their flowers.

Because of the unusual morphology of milkweed flowers, their pollination by insect vectors is much more complex than is usually found in most other types of flowers. In order to better understand the insects that have evolved to pollinate them, it is important to understand the morphology of these flowers, the morphology of the pollium, and the mechanism of pollination.

Morphology of Milkweed Flowers

In *Asclepias*, the flowers are arranged in rounded or flat clusters called umbels. Depending on the species, these umbels in turn are arranged either at the tip of the stem (terminal) or along its sides (lateral). The central part of each flower consists of a short five-sided column containing five fused male filaments surrounding two female pistils and topped by a fleshy stigma head (or style table) (Figure 1). This column in turn is encircled by the most conspicuous and colorful part of the flower (corolla), consisting of 5 nectar-containing hoods. These hoods are composed of united petals, each with (or without depending on the species) an incurved horn. This corolla in turn is surrounded by 5 deflexed usually brightly-colored sepals. Stigmatic slits, bordered by two parallel corneous anther wings, are found on each of the five sides of the column between the five hoods. The opening between these anther wings leads into the stigmatic chamber (Corry 1883, Frye 1902, and Brookman 1981).

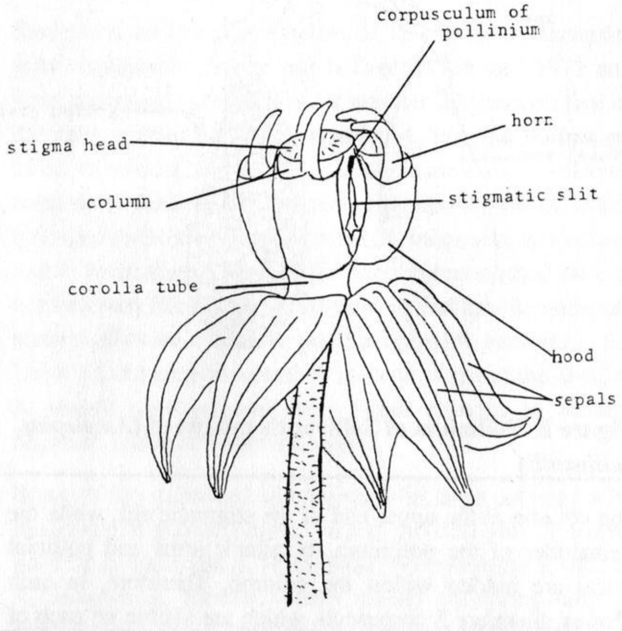

Figure 1. Flower of poke milkweed (*Asclepias exaltata*)

Morphology of the Pollinium (or Pollinarium)

Each stamen has two flattened pyriform pollinial sacs, each of which contains a waxy pollen mass of approximately 500 pollen grains (Figure 2). Each pollinial sac is attached to a translator arm (or retinacula) with a characteristic knee bend. The translator arms of two adjacent pollinial sacs of different anthers in turn are joined together to a blackish-brown oval corpusculum (or gland) with a dorsal medial slit. Two pollinial sacs, together with their translator arms and a central common corpusculum, constitutes a pollinium (or pollinarium). Only the corpusculum is visible on the outer surface of

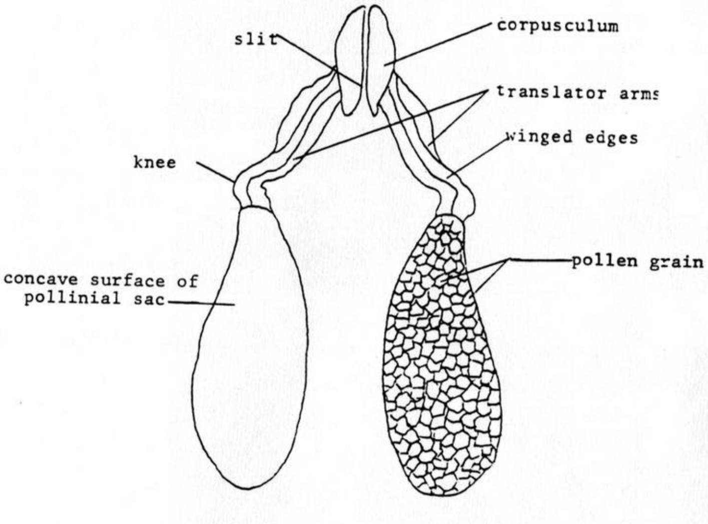

Figure 2. Pollinium of Sullivant's milkweed (*Ascelepias sullivantii*)

the column at the upper end of the stigmatic slit, while the remainder of the pollinium (translator arms and pollinial sacs) are hidden within the column. Therefore, in each flower, there are 5 corpuscula which are visible on each of the 5 sides of the column, and 10 pollen sacs which are hidden in each column (Brookman 1981).

Pollination of Milkweed Flowers

The pollination of *Asclepias* flowers involves two separate steps: (1) the extraction of a pollinium with its two pollinial sacs from a donor flower and (2) the insertion of one of the these pollinial sacs into a stigmatic chamber of a recipient flower. The first step is accomplished in the following manner. As the insect pollinator feeds on the nectar in the hoods of a donor flower, a leg may be guided upward by the two parallel anther wings of a stigmatic slit toward a projecting corpusculum. With further movement upward, a bristle or hair may wedge in the fine dorsal slit in the corpusculum of the pollinium which may then be pulled out (or extracted) from the column. When first extracted the pollinial sacs have their flat sides lying perpendicular to the stigmatic slit and cannot be inserted into the stigmatic chamber of a receptor flower in this position.

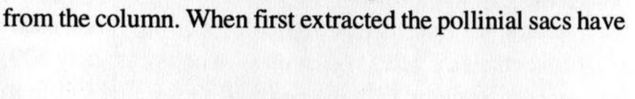

Figure 3. Hind leg of honey bee (*Apis mellifera*) with attached pollinal chain.

The second stage of pollination begins with the drying of the withdrawn pollinium's translator arms while attached to the pollinator's appendage or body hairs. This causes the pollinia to turn inward 90 degrees and results in the concave surface of these pollinial sacs to face downward. The pollinial sacs in this position are now in the same plane as that of a stigmatic slit and can now be inserted into a stigmatic chamber of a recipient flower. The same leg movements that were responsible for the removal of the pollinium from the donor flower causes the leg to be guided upward along the stigmatic slit of a recipient flower. The corpusculum, attached to the pollinator's hair, does not enter the stigmatic slit of the recipient flower, but slides over its anther wings. The first part of the pollinium to enter the stigmatic chamber is the right-angled bend in the translator arm (knee bend), followed by the remainder of the translator arm with the pollinial sac following behind. The pollinial sac with its translator arm is moved upward inside the stigmatic chamber, eventually reaching the superior end of the stigmatic slit. Following the wedging of the pollinial sac in the stigmatic chamber, the further upward movement of the pollinator's leg causes the translator arm to break off. This leaves the pollinial sac in the stigmatic chamber (Robertson 1886, Betz personal observations).

Chain formation may result immediately after the insertion of a pollinial sac into the stigmatic chamber by the continued upward movement of the pollinator's leg. The broken remainder of the translator arm is directed toward the projecting corpusculum at the top of the stigmatic slit, and this flattened broken translator arm wedges into the dorsal slit of the corpusculum. Thus, with the continued upward movement of the leg, a new pollinium is extracted from the flower, producing a chain or cluster of three pollinial sacs. The recipient flower now has become a donor flower. Broken and intact translator arms of chains and clusters of pollinia can act as new attachment sites for other pollinia, forming all sorts of straight and branching chains of pollinia. It is probable that these pollinial chains also increase the likelihood of the insertion of a pollinial sac into a stigmatic chamber of a receptor flower as compared to the situation in which a single pollinium is attached to a body or appendage hair.

Many of the insects found on *Asclepias* flowers are not pollinators of those flowers. Some insects (visitors) visit the flowers to suck nectar, but they almost never extract pollinia. These are recognized as non-pollinators and are sometimes designated as "nectar thieves" (Willson et al. 1979). Others (pollen extractors) may extract pollinia from donor flowers, but they almost never insert a pollinial sac into a recipient flower. The pollen inserters (or actual pollinators) of *Asclepias* flowers are those insects that complete both of the two important processes of pollination: (1) the extraction of two pollinial sacs from a donor flower; and (2) the insertion of at least one of these pollinial sacs into the stigmatic chamber of a recipient flower. In all studies these latter two groups (pollen extractors and pollen inserters) are lumped together into "pollen vectors".

In Europe insect species collected on the flowers of *Asclepias syriaca*, an introduced species, were compiled by Delpino (1867), Hildebrand (1866), and Mueller (1873, 1882). No distinctions were made as to which ones were visitors, pollen extractors, or pollen inserters.

In North America, most studies carried out on the insect visitors of *Asclepias* distinguished between visitors and those observed carrying pollinia (pollen extractors), but did not differentiate between pollen extractors and pollen inserters. Robertson (1886, 1887a, 1887b, 1891, 1895, and 1929) carried out extensive studies on the insect visitors to the flowers of eight North American *Asclepias* species found in southwestern Illinois (*A. hirtella, A. incarnata, A. purpurascens, A. sullivantii, A. syriaca, A. tuberosa, A. verticillata*, and *A. viridiflora*). He distinguished between those that were pollinia extractors and those that were not (visitors). Macior (1965) studied the bees and wasps carrying pollinia of three species in southeastern Wisconsin (*A. incarnata, A. syriaca*, and *A. verticillata*). He recorded the frequency and location of the corpuscula on various parts of the body and distinguished between those attached directly to body parts (basal) or in chains to translator arms of other corpuscula (distal). Frost (1965) studied the insect visitors to three species of milkweeds in Pennsylvania (*A. incarnata, A. syriaca*, and *A. tuberosa*) and recorded the number and attachment of the pollinia carried on various body parts (mouth, claws, pulvilli, tibiae, and tarsi). Willson et al. (1979) in central Illinois recorded the insect visitors to *A. verticillata*. They listed those species that were carrying pollinia and reported the average number of pollinia carried. Willson and Bertin (1979) in central Illinois listed the insect visitors to *A. syriaca* and also identified those species carrying pollinia along with the average number of pollinia being carried.

Thus, in the absence of definitive information, this present study was primarily undertaken to distinguish the pollen inserters from the pollen extractors of *Asclepias* flowers. In addition, the points of attachment of the pollinia to the body hairs and appendages of the pollinators were also determined in order to record similarities and differences among insect species carrying pollinia from the same or different species of *Asclepias*. Due to the relatively low extraction and insertion of pollinial sacs into *Asclepias* flowers by many native insects compared to that of the exotic honey bee (*Apis mellifera*), speculations are made concerning the pre-settlement pollinators of *Asclepias* flowers.

METHODS

Studies on the insect pollinators of 12 species of *Asclepias* were extensively carried out between 1965 and 1971 and were continued sporadically for another 20 years on five of the rarer species (*A. amplexicaulis, A. hirtella, A. lanuginosa, A. meadii*, and *A. viridiflora*). Insects were collected from more than 40,000 milkweed plants, 93.8% of which belonged to three common species (*A. incarnata, A. syriaca*, and *A. verticillata*). Most of the populations studied were in northeastern Illinois and northwestern Indiana. In addition, some studies were done on populations of *A. exaltata* in the Devil's Lake area of central Wisconsin. Most of the data for *A. meadii* were gathered from plants growing in western Missouri and northeastern Kansas.

Some of the milkweed species grew in large colonies with thousands of plants (ramets) as was the case with *A. incarnata, A. syriaca*, and *A. verticillata*. Whereas others, such as *A. lanuginosa*, formed smaller clones consisting only of hundreds of plants. Other species, such as *A. sullivantii*, grew in isolated populations consisting of a half-dozen plants. Still others, such as *A. hirtella, A. meadii* and *A. viridiflora*, grew as isolated plants (genets) or small clusters of two or three plants.

Populations of *Asclepias* were visited throughout the blooming season which usually lasted about two or three weeks depending on the species. Insects were collected from flowers by netting two to four times per week for periods of one to five hours at variable times throughout the day. A few attempts to collect insects nocturnally from some milkweeds were made, but no insects were taken. Insect specimens were brought back to the laboratory, pinned, and, in most cases, identified to species. Corroborating identifications were also made through the use of the insect collections at the Field Museum of Natural History, Chicago, Illinois.

The identified insects were checked under a dissecting microscope for the number of corpuscula they carried, as well as for the points of attachment of the corpuscula to the body or appendage hairs and bristles. In addition, the number of pollinial sacs still attached to the translator arms (i.e., whether 0, 1, or 2 sacs) was recorded.

The number of pollinial sacs extracted from a donor flower by a pollinating insect was determined by first noting the number of corpuscula attached directly to the body hairs and

Table 1. Percentage of Presumed Pollen Sac Insertion in *Asclepias*.

Milkweed Species & Insect Vector (#) = sample size	# Pollinial Sacs Extracted by Species from Donor Flowers of	% Pol.Sacs Inserted into Recipient Flowers of	Mean # Pol. Sacs Extracted for Insect Species on
A. amplexicaulis			
Apis mellifera (1)	0	00.0	00.0
Megachile brevis (3)	0	00.0	00.0
A. exaltata			
Apis mellifera (6)	62	85.5	10.3
Bombus pennsylvanicus (18)	54	88.9	3.0
Ancyloxipha numitor (2)	4	25.0	2.0
Epargyreus clarus (3)	2	0.0	0.7
Lasius niger (50)	4	25.0	0.1
A. hirtella			
Bombus affinis (2)	182	51.6	91.0
Bombus griseocollis (2)	64	38.0	32.0
A. incarnata			
Apis mellifera (23)	2068	74.2	89.9
Bombus griseocollis (32)	1484	80.4	46.4
Bombus nevadensis auricom(6)	564	72.5	94.0
Papilio sp. (7)	384	75.0	54.9
Sphex ichneumoneus (26)	1904	79.4	73.2
Sphex pennsylvanicus (14)	1794	75.8	128.1
Colias philodice (4)	46	71.8	11.5
Danaus plexipus (5)	66	75.8	13.2
Limenitis archippus (6)	98	64.3	16.3
Megachile latimonas (3)	48	25.0	16.0
Pieris rapae (4)	24	58.3	6.0
A. lanuginosa			
Colletes armatus (1)	8	37.5	8.0
Megachile mendica (1)	0	0.0	0.0
A. meadii			
Anthophora abrupta (6)	26	42.3	4.3
Apis mellifera (1)	0	0.0	0.0
Bombus affinis (1)	4	0.0	4.0
Bombus griseocollis (1)	2	0.0	2.0
A. purpurascens			
Apis mellifera (30)	480	83.3	16.0
Bombus pennsylvanicus (6)	12	58.3	2.0
A. sullivantii			
Apis mellifera (120)	1428	77.9	11.9
Bombus fervidus (7)	42	90.5	6.0
Bombus pennsylvanicus (20)	160	86.9	8.0
Sphex ichneumoneus (1)	18	83.3	18.0

Table 1, continued.

Milkweed Species & Insect Vector (#) = sample size	# Pollinial Sacs Extracted by Species from Donor Flowers of	% Pol.Sacs Inserted into Recipient Flowers of	Mean # Pol. Sacs Extracted for Insect Species on
A. syriaca			
Apis mellifera (275)	7776	60.9	28.3
Bombus pennsylvanicus (865)	4	0.0	0.0
Sphex ichneumoneus (1)	4	75.0	4.0
A. tuberosa			
Apis mellifera (69)	1138	71.5	16.5
Bombus pennsylvanicus (14)	24	50.0	2.0
Sphex ichneumoneus (2)	218	83.5	109.0
Colletes armatus (7)	8	75.0	1.1
Danaus plexippus (6)	2	50.0	0.3
Lygaeus kalmii (25)	2	0.0	0.1
Mechachile brevis (20)	10	70.0	0.5
Strymon titus (6)	8	0.0	1.3
A. verticillata			
Apis mellifera (12)	342	32.2	28.5
Bombus griseocollis (7)	230	64.8	32.9
Myzinum quinquecintum (15)	654	52.1	43.4
Polistes fuscatus (2)	298	33.6	149.0
Prionyx atratus (2)	34	35.6	17.0
Sphex ichneumoneus (11)	114	60.5	10.4
Sphex pennsylvanicus (12)	424	53.3	35.3
Tachytes mandibularis (4)	40	30.0	10.0
Colletes compactus (2)	84	10.7	42.0
Ceratogastra ornata (2)	16	25.0	32.0
Epibembex nubilipennis (2)	4	50.0	2.0
Megachile latimanus (1)	4	75.0	4.0
A. viridiflora			
Bombus griseocollis (5)	176	39.8	35.2

in the pollinial chains. Since each corpusculum has two pollinial sacs attached to it, the total number of pollinial sacs extracted by a pollinating insect from donor flowers is double the number of corpuscula. However, more pollinia may have been extracted, but have been lost. This can occur by accidental breakage of a chain or by being brushed off by an insect cleaning itself. Thus, the actual number of pollinia extracted may be more. For this reason, this calculated number of extracted pollinial sacs is a presumed number. Table 1 shows the total number of extracted pollinial sacs for each insect species observed in this study.

The number of pollinial sacs inserted into a recipient flower by a pollinating insect was determined by subtracting the number of pollinial sacs still attached to translator arms from the total number of pollinial sacs calculated to have been extracted from donor flowers. Since some pollinial sacs may have been accidentally lost for reasons other than being used in pollination, the number of inserted pollinial sacs actually may have been different from the computed one. Thus, the number of inserted pollinial sacs computed is a presumed number.

Using these data, the total number of pollinial sacs inserted into the stigmatic chambers of recipient flowers was con-

Table 2. Insect Pollinators of *Asclepias* and the Species Pollinated.

Species	Family	Milkweed Pollinated
HYMENOPTERA		
Bees		
Anthophora abrupta (digger bee)	Anthophoridae	*A. meadii.*
Apis mellifera (honey bee)	Apidae	*A. amplexicaulis* *A. exaltata* *A. incarnata* *A. meadii* *A. purpurascens* *A. sullivantii* *A. syriaca* *A. tuberosa* *A. verticillata*
Bombus affinis (bumble bee)	Apidae	*A. affinis* *A. meadii*
Bombus fervidus (bumblebee)	Apidae	*A.sullivantii*
*Bombus griseocollis (*prairie bumblebee)	Apidae	*A. hirtella* *A. incarnata* *A. meadii* *A. verticillata* *A. viridiflora*
Bombus nevadensis auricomus (bumblebee)	Apidae	*A. incarnata*
Bombus pennsylvanicus (bumblebee)	Apidae	*A. exaltata* *A. purpurascens* *A. sullivantii*
Colletes armatus (plasterer bee)	Colletidae	*A. lanuginosa* *A. tuberosa*
Colletes compatus (plasterer bee)	Colletidae	*A. verticillata*
Megachile brevis (leafcutting bee)	Megachilidae	*A. tuberosa*
Megachile latimanus (leafcutting bee)	Megachilidae	*A. incarnata* *A. verticillata*
Megachile mendica (leafcutting bee)	Megachilidae	*A. lanuginosa*
Wasps		
Ceratogastra ornata (ichneumonfly)	Ichneumonidae	*A. verticillata*
Epibembix nubilipennis	Sphecidae	*A. verticillata*
Myzinum quinquecintum (five-banded tiphiid wasp)	Tiphiidae	*A. verticillata*
Polistes fuscatus (northern paper wasp)	Vespidae	*A. verticillata*
Prionyx atratus (thread-waisted wasp)	Sphecidae	*A. verticillata*

Table 2, continued.

Species	Family	Milkweed Pollinated
Sphex ichneumoneus (great golden thread-waisted wasp)	Sphecidae	*A. incarnata* *A. sullivantii* *A. tuberosus* *A. verticillata*
Sphex pennsylvanicus (great black thread-waisted wasp)	Sphecidae	*A. incarnata* *A. verticillata*
Tachytes mandibularis (thread-waisted wasp)	Sphecidae	*A. verticillata*
Lepidoptera/Butterflies		
Ancyloxipha numitor (least skipper)	Hesperiidae	*A. exaltata*
Colias philodicee (common sulfur butterfly)	Pieridae	*A. incarnata*
Danaus plexippus (monarch butterfly)	Danaidaee	*A. incarnata* *A. tuberosa*
Epargyreus clarus (silver spotted skipper)	Hesperiidae	*A. exaltata*
Limenitis archippus (viceroy)	Nymphalidae	*A. incarnata*
Papilio polyxenes (black swallowtail)	Papilionidae	*A. incarnata*
Pieris rapae (cabbage butterfly)	Pieridae	*A. incarnata*
Strymon titus (coral hairstreak)	Lycaenidae	*A. tuberosa*

verted into a percentage of the total number of pollinial sacs extracted from donor flowers (Table 1).

The mean number of pollinial sacs extracted was calculated for the sample population of each insect species found in association with a particular *Asclepias* species. This mean was used as a measure of the ability of a species to extract pollinial sacs from donor flowers (Table 1).

Even though the percentages and means as calculated above are based on presumed numbers, it is felt that these derived data are still useful for comparative purposes. They provide a basis for understanding the relative effectiveness of the various insects observed in this study as pollinators for the different species of milkweeds.

RESULTS

One thousand seven hundred and fifty two insect specimens, representing 28 species and belonging to 10 different families, were collected and reported in this study (Tables 1 and 2). Three groups, the larger bees, wasps, and butterflies were the most important groups in pollinating *Asclepias* flowers. These groups of insects were important because they extracted large numbers of pollinial sacs from donor flowers, and inserted a high percentage of these pollinial sacs into the stigmatic chambers of recipient flowers. The two most important families of bees were the *Apidae*: honey bees (*Apis*) and bumble bees (*Bombus*), and the *Anthophoridae*: mining bees (*Anthophora*). Among the important families of wasps, were the *Sphecidae*: thread-waisted wasps (*Sphex, Prionyx*, and *Tachytes*); *Vespidae*: paper wasps (*Vespa*); and the *Tiphiidae* (*Myzinum*). Important butterflies include the *Papilionaceae*: swallowtails (*Papilio*) and *Nymphalidae* (brushfooted butterflies). *Apidae, Sphecidae*, and *Papilionaceae* were the only families pollinating *A. exaltata* (poke milkweed), *A. hirtella* (tall green milkweed), *A. meadii* (Mead's milkweed), *A. purpurascens* (purple milkweed), *A. sullivantii* (Sullivant's milkweed), and *A. viridiflora* (short green milkweed). For most of the other milkweeds this group of three families constituted at least 90% of the pollinators. For example, in *A. incarnata* (marsh milkweed) this group accounted for 97.3% of the pollination as well as 98.8% in *A. tuberosa* (butterfly weed) and 98.2% in *A. verticillata* (whorled milkweed).

Table 3. Attachment of Pollinia to appendages of *Bombus sp.* **pollinating** *Asclepias viridiflora, A. hirtella* **and** *A. exaltata.*

Insect Appendage	*B.griseocollis* (*A. viridiflora*) (5)		*B.affinis* (*A. hirtella*) (2)		*B.griseocollis* (*A. hirtella*) (2)		*B. pennsylvanicus* (*A. exaltata*) (18)	
	Ext	Ins	Ext	Ins	Ext	Ins	Ext	Ins
Mouth Parts	2	1	0	0	6	3	6	3
Claws								
front	0	0	0	0	0	0	0	0
middle	0	0	0	0	0	0	0	0
hind	0	0	0	0	0	0	0	0
Pulvilli								
front	0	0	0	0	0	0	0	0
middle	0	0	0	0	0	0	0	0
hind	0	0	0	0	0	0	0	0
Tarsi								
front	24	16	18	13	2	1	16	16
middle	76	38	16	9	0	0	18	17
hind	56	14	10	10	0	0	14	12
Tibiae								
front	2	0	16	8	4	1	0	0
middle	16	1	24	10	20	14	0	0
hind	0	0	56	28	4	0	0	0
Femur								
front	0	0	0	0	0	0	0	0
middle	0	0	4	1	4	1	0	0
hind	0	0	10	4	0	0	0	0
Trochanter								
front	0	0	0	0	0	0	0	0
middle	0	0	10	5	12	1	0	0
hind	0	0	4	2	0	0	0	0
Coxa								
front	0	0	2	0	0	0	0	0
middle	0	0	2	0	8	2	0	0
hind	0	0	0	0	0	0	0	0
Thorax	0	0	8	4	4	0	0	0
Abdomen	0	0	2	0	0	0	0	0
Total	176	70	182	94	64	23	54	48
% Transfer	(39.8)		(51.6)		(38.0)		(88.8)	

Ext = Extracted; Ins = Inserted; Sample size (in parentheses).

Table 4. Attachment of Pollinia to body parts of *Apis mellifera* pollinating different species of *Asclepias*

	A. purpurascens (30)		*A.sullivantii* (120)		*A.incarnata* (23)		*A.tuberosa* (69)	
	Ext	Ins	Ext	Ins	Ext	Ins	Ext	Ins
Mouth Parts	0	0	70	10	98	63	0	0
Claws								
front	6	5	194	134	180	144	20	14
middle	2	2	322	265	194	149	84	67
hind	2	2	336	277	142	122	96	83
Pulvilli								
front	108	77	160	136	272	228	30	26
middle	158	142	206	171	184	155	94	74
hind	152	141	134	115	108	98	58	45
Tarsi								
front	4	1	0	0	222	151	70	39
middle	20	14	0	0	338	243	174	117
hind	28	16	0	0	268	171	172	118
Tibiae								
front	0	0	0	0	0	0	8	2
middle	0	0	4	3	0	0	22	17
hind	0	0	2	1	52	3	310	212
Totals	480	400	1428	1112	2058	1527	1138	814
%Transfer	(83.3)		(77.9)		(74.2)		(71.5)	

Ext = Extracted; Ins = Inserted; Sample size (in parentheses).

Families of lesser importance for pollination were the leaf-cutting bees *Megachilidae*: (*Megachile*); plasterer bees *Colletidae* (*Colletes*); *Ichneumonidae*: ichneumon wasps (*Ceratogastra*); *Danaidae*: monarch butterflies (*Danaus plexipus*); *Hesperiidae* skippers (*Ancyloxipha*); *Nymphalidae*: viceroys (*Limenitis*) and *Pieridae*: sulfurs (*Pieris*). (Table 1 and 2).

Many insects, such as the cerambycid milkweed beetles (*Tetraopes tetraophthalmus* and *T.femoratus*), are commonly found on milkweed flowers but they are usually not pollinators (Robertson 1927 and Betz personal observations). In addition, the monarch butterfly (*Danaus plexippus*), a common visitor to *Asclepias* flowers, appears to be a minor pollinator in only two species (*A. incarnata* and *A. tuberosa*), in that it extracts and inserts relatively few pollinial sacs.

Pollination Characteristics

Points of Corpuscula Attachment.

The point of attachment of the corpusculum and pollinia to the body and appendage hairs, and to the bristles of an specimen varied depending on the insect species and the *Asclepias* species being pollinated (Tables 3, 4, 5, and 6). Most of the pollinia were attached to the lower parts of the appendages, i.e., the hairs on the tarsi and tibia, pulvilli bristles, and claws (Figure 3). Very few were attached to the mouth (palpi and tongue). In a special case involving the bumble bees (*Bombus griseocollis* and *B.affinis*) found on the tall green milkweed (*A. hirtella*), the pollinia were not only attached to hairs and bristles of lower leg appendages, but also further up on the leg and closer to the body, i.e., femur, trochanter and coxa. Some were even on the thorax and abdomen (Table 3). This may be due in part to the fact that the umbels of small flowers in *A. hirtella* are loose with relatively long and thin pedicels. It is possible that when sucking nectar the bumble bee sinks down into the mass of flowers and extracts pollinia using hairs and bristles closer to its body.

Number of Pollinial Sacs Extracted.

The mean number of pollinial sacs extracted from donor flowers by a pollinating species varied, depending on both the insect species and the species of *Asclepias* (Table 1). The insect species extracting the highest number of pollinial sacs was the paper wasp (*Polistes fuscatus*). They were collected from *A. verticillata* and had a mean of 149.0 extracted pollinial sacs. The great black thread-waisted wasp (*Sphex pennylvanicus*) found on *A. incarnata* had a mean of 128.1. In contrast, the great golden thread-waisted wasp (*Sphex ichneumoneus* found on *A. verticillata* extracted only a mean of 10.4 pollinial sacs. The monarch butterfly (*Danaus plexippus*) collected from *A. tuberosa* had only a mean of 0.3 pollinial sacs.

The number of pollinial sacs extracted by specimens within a species varied widely. Of the two specimens of *B. griseocollis* collected on *A. hirtella*, one carried 40 pollinial sacs, while the other carried 24. Of ten specimens of honey bee (*Apis mellifera*) collected on *A. syriaca*, one carried 92 pollinial sacs, and second 50, a third 4, six specimens carried 2, and one specimen none at all.

Percent Insertion of Pollinial Sacs.
The highest percentages of pollinial sacs inserted by a species was found among the bumble bees (*Bombus*). The black-banded bumble bee (*B. fervidus*) inserted 90.5% of the pollinial sacs in the pollination of *A. sullivantii. Bombus pennsylvanicus* inserted 88.9% of the pollinial sacs in the pollination of *A. exaltata* (Table 1).

Pollinators by Plant Species
Asclepias amplexicaulis (sand milkweed). Observations on 178 flowering stems of this milkweed during two growing seasons resulted in the collection of only two species of insects: one honey bee (*Apis mellifera*) and three (two males and one female) leaf-cutting bees (*Megachile brevis*) (Table 1). None of the four specimens had extracted pollinial sacs. Thus it is unlikely that these were major pollinators of this milkweed species. Further studies need to be undertaken on this species.

A. exaltata (poke milkweed). Observations made on 440 flowering stems of this milkweed during two growing seasons resulted in the collection of two species of insects which had extracted and inserted pollinial sacs (Table 1). Of the eighteen specimens of *Bombus pennsylvanicus* examined, 8 carried pollinial sacs principally on the tarsal hairs (Table 3). Eighty-nine percent of the extracted 54 pollinial sacs were inserted. Of the six honey bees (*Apis mellifera*) examined, two also carried pollinial sacs principally on the pulvilli. Eighty-six percent of the extracted 62 pollinial sacs were inserted.

Three specimens of silver spotted skipper (*Epargyreus clarus*) were collected, but only one carried two pollinial sacs. None of these was inserted. Two specimens of the least skipper (*Ancyloxipha numitor*) carried 4 pollinial sacs, and only one was inserted. In addition, many tiny Diptera and robber flies (*Erax rufilabris*) were seen to visit the flowers, but none carried pollinial sacs.

A. hirtella (tall green milkweed). Observations on 58 stems of this milkweed over two growing seasons resulted in the collection of only two species of bumble bees (Table 1). The two specimens of *B. affinis* inserted 51.6% of the 182 pollinial sacs they originally extracted. The two specimens of *B. griseocollis* collected had inserted 38.0% of the 64 pollinial sacs extracted from recipient flowers. Although the largest numbers of corpuscula in both of these species were attached to the hairs of the tibia and tarsi, substantial numbers were also attached to the hairs of the femur, trochanter, coxa, thorax, and abdomen.

A. incarnata (marsh or swamp milkweed). Observations on 10,500 stems of this milkweed over two blooming seasons indicated that large numbers of a variety of insects were attracted to the flowers of this species (Table 1). The 23 specimens of honey bee (*A. mellifera*) collected inserted 74.2% of the extracted 2068 pollinial sacs. Most of these pollinial sacs were carried on the claws, pulvilli, and tarsal hairs, but they were also carried to a lesser extent on the tibial hairs (Table 4). The 32 specimens of *B. griseocollis* collected inserted 80.4% (1193) of the extracted 1484 pollinial sacs. The 6 specimens of *B. nevadensis auricomis* inserted 72.5% (409) of 564 pollinial sacs extracted. Most of the corpuscula were attached to the tarsal hairs, but they were also attached to the claws, pulvilli and tibial hairs. The leaf-cutting bee *Megachile latimanus* appeared to be a minor pollinator of this milkweed (Table 1).

The 26 specimens of the golden thread-waist wasp (*Sphex ichneumoneus* collected from *A. incarnata* inserted 79.4% of the pollinial sacs of the extracted 1904 pollinial sacs, while the black thread-waist wasp (*S. pennsylvanicus*) inserted 75.8% of the extracted 1794 pollinial sacs. In both species most of the pollinial sacs were carried on the tarsal claws, but a substantial number were also carried on the mouth, claws, pulvilli and tibial hairs in both species (Table 5).

Among the butterflies collected, 6 specimens of the viceroy (*Limenitis archippus*) inserted 64.3% of the 98 extracted pollinial sacs, while the 5 specimens of the monarch (*Danaus plexippus*) inserted 75.8% of the 66 extracted pollinial sacs. The 7 specimens of the black swallowtail (*Papilio polyxenes*) inserted 75.0% of the 384 extracted pollinial sacs. Other species of butterflies collected included 6 specimens of the common sulfur (*Colias philodice*) and 4 specimens of the cabbage butterfly (*Pieris rapae*). Most of the corpuscula were attached to the tarsal hairs for all of these *Lepidoptera* (Table 6).

Table 5. Attachment of Pollinia to body parts of *Sphex sp.* wasps pollinating *Asclepias*.

	Sphex ichneumoneus		*Sphex pennsylvanicus*		*Sphex ichneumoneus*		*Sphex pennsylvanicus*	
	(*A.incarnata*)				(*A.verticillata*)			
	(26)		(14)		(11)		(12)	
	Ext	Ins	Ext	Ins	Ext	Ins	Ext	Ins
Mouth Parts	48	27	12	11	0	0	0	0
Claws								
front	32	25	30	23	4	0	0	0
middle	8	6	2	1	2	1	0	0
hind	6	5	8	6	4	1	0	0
Pulvilli								
front	50	43	26	22	2	0	16	3
middle	16	14	4	3	8	5	0	0
hind	18	9	6	5	2	0	6	4
Tarsi								
front	874	707	810	604	62	46	278	140
middle	392	324	508	419	24	14	66	32
hind	414	321	370	257	6	2	58	37
Tibiae								
front	20	13	12	5	0	0	0	0
middle	16	10	2	1	0	0	0	0
hind	10	8	4	2	0	0	0	0
Totals	1904	1512	1794	1359	114	69	424	226
% Transferred	(79.4)		(75.8)		(60.5)		(53.3)	

Ext = Extracted; Ins = Inserted; Sample size (in parentheses).

A. lanuginosa (woolly milkweed). Observations on 255 flowering stems of this milkweed during two blooming seasons resulted in the collection of only two specimens (Table 1). One, a colletid bee (*Colletes armatus*), carried 8 pollinia on the tarsal hairs of the second and third pairs of legs. Three pollinia were incomplete and may have been inserted. The leaf-cutting bee (*Megachile mendica*), bore no pollinia (Table 1). Many tiny *Diptera* and wingless *Formicidae* (ants) were observed on the flowers, but none of the many examined had pollinial sacs attached. Several specimens of *Bombus griseocollis* were present in the vicinity of the blooming plants, but were not observed to visit the flowers or carry pollinial sacs.

A. meadii (Mead's milkweed). Few pollinators were observed on 140 flowering stems of this milkweed during nine blooming seasons. Two bumble bee queens (*B. affinis* and *B. griseocollis*) were collected, but were not found to have attached pollinia. Six specimens of the mining bee (*Anthophora abrupta*) were collected that had extracted 26 pollinial sacs, of which 11 (42.3%) had been inserted (Table 1). Ants (*Formicidae*) were commonly observed feeding on the nectar dripping from the nectaries, but they carried no pollinia.

A. purpurascens (purple milkweed). Observations made on 65 flowering stems of this milkweed during two blooming seasons resulted in the collection of 30 specimens of the exotic honey bee (*Apis mellifera*). This exotic bee species appears to be the major pollinator of this milkweed species. Six specimens carried 480 extracted pollinial sacs, of which 399 (83.1%) were inserted. Seven specimens of *Bombus pennsylvanicus* were also collected. Three of them extracted 12 pollinial sacs. Only 7 of these pollinial sacs (53.3%) were inserted (Table 1).

A. sullivantii (prairie milkweed). Observations on 575 flowering stems of this milkweed during two blooming seasons resulted in the collection 120 specimens of the exotic honey bee (*Apis mellifera*). This insect far outnumbered the other insect species observed visiting this milkweed (Table 1). Out of 1428 extracted pollinial sacs 77.8% (1112) were missing and inserted. The pollinia (94.7%) were attached to the claws and pulvilli (Table 4).

In addition to honey bees, two species of bumble bees were collected on flowers of this plant. Twelve specimens of *Bombus pennsylvanicus* out of the 20 collected carried pollinia. Ninety-five percent of the 160 pollinial sacs extracted were on their claws. Of these, 86.9% (152) were inserted (Table 3). Seven specimens of *B. fervidus* were also collected on this milkweed, of which three were found to be carrying 42 pollinial sacs. In this species 90.5% (38) were inserted.

One specimen of the great golden thread-waisted wasp (*Sphex ichneumoneus*) was also collected on *A. sullivantii*. Of the 18 extracted pollinial sacs of this milkweed, 83.3% (15) were inserted. In addition, it also carried a large number of pollinia from the smaller marsh milkweed (*A. incarnata*) which grew nearby. It is interesting to note that some of the pollinia from *A. sullivanti* carried by this wasp were attached to ligaments (broken translator arms) of *A. incarnata*. These in turn were attached in chains to the relatively large pulvillus of this wasp.

At one site other species of wasps were seen visiting a colony of *A. incarnata* not more than 20 feet away from *A. sullivantii*, but many spot-checks on the kind of pollinia carried by these wasps showed that most did not visit the larger flowers of *A. sullivantii*. Those that did, did not pick up any pollinia.

Small *Diptera* and *Lasius niger*, a wingless ant, were also observed on flowers of *A. sullivantii*, but they were too small to be pollinators and carried no pollinia. Occasionally a monarch (*Danaus plexippus*) or cabbage butterfly (*Pieris rapae*) was seen to visit the blooms, but none was found to carry enough pollinia to be an effective pollinator.

A. syriaca (common milkweed). Observations on 12,000 flowering stems of this milkweed were carried out through two blooming seasons. The exotic *Apis mellifera* was by far the major pollinator of this milkweed. Almost all of the 275 specimens of *Apis mellifera* collected on this species carried pollinia. The corpuscula were almost exclusively attached to two body parts: (1) the pulvilli (91.6%) and (2) the mouth parts (8.4%). Of the 7776 pollinial sacs extracted, 4736 (60.9%) were inserted (Table 1).

Eight hundred and sixty-five specimens of *Bombus pennsylvanicus* also were caught on the flowers of this species but only two were found to be carrying pollinia, i.e., one intact pollinia each. A variety of sphecid wasps and butterflies, including the monarch (*Danaus plexippus*), hair streaks (*Strymon sp.*), and skippers (*Epargyreus sp.*), were also collected, but these carried no pollinia. The one specimen of *Sphex ichneumoneus* caught had extracted four pollinial sacs, three of which were inserted.

A. tuberosa (butterfly weed). Observations on 865 flowering stems of this milkweed were carried out through two blooming seasons. As with many of the other species of *Asclepias*, the exotic *Apis mellifera* was the major pollinator for this milkweed. Sixty-nine specimens of this species, carrying 1138 pollinial sacs, were collected from its flowers over two blooming seasons (Table 1). There were 814 pollinial sacs (71.5%) inserted. More than two-thirds of the corpuscula were attached to the tarsal hairs (36.6%) and tibial hairs (29.9%).

Fourteen specimens of *B. pennsylvanicus* were collected on the flowers of *A. tuberosa*. Five of these carried 24 pollinial sacs, of which 12 (50.0%) were inserted. Two specimens of the great golden thread-waisted wasp (*Sphex ichneumoneus*) were collected, each of which carried over 90 pollinial sacs. Of the 218 pollinial sacs extracted, 83.5% (182) were inserted.

Twenty specimens of the leaf cutting bee (*Megachile brevis*) were collected. Only two of these twenty carried pollinial sacs. One specimen carried 4 and the other 6. Only 3 of these were inserted. The little plasterer bee (*Colletes armatus*) was frequently seen visiting the flowers of this milkweed, but only one of the 7 specimens collected carried pollinial sacs. Of the eight pollinial sacs extracted, 6 were inserted.

Many tiny flies (*Diptera*) and wingless ants (*Formicidae*) were observed visiting the flowers, yet none carried pollinia. Butterflies visited the flowers frequently. The hairstreak (*Strymon acadica*) and the monarch (*Danaus plexippus*) were among those observed, but they were almost always free of pollinia. If a pollinium was present, it was usually complete with two pollinial sacs. Many lesser milkweed bugs (*Lygaeus kalmii*) were examined, but only one was found carrying one complete pollinium.

A. verticillata (whorled milkweed). Based on the observations of 15,000 flowering stems over a period of two blooming seasons there appears to be no major pollinator of this milkweed (Table 1). This is in accordance with the work of Willson, Bertin and Price (1979). Thirteen species were collected on it. The most numerous pollinators were the honey bee (*Apis mellifera*), the five-banded tiphiid wasp (*Myzinum quinquecintum*) and the thread-waisted wasps (*Sphex ichneumoneus* and *S. pennsylvanicus*).

Many species of small bees and wasps were common visitors. Lepidoptera were fewer in number and generally smaller in

Table 6. Attachment of Pollinia to the body parts of the swallowtail (*Papilio polyxenes*), the bee (*Anthophora abrupta*), and the wasp (*Myzinum quinquecinctum*) pollinating *Asclepias*.

Body Part	*Papilio polyxenes* (7) *A.incarnata*		*Limenitis archippus* (6) *A.incarnata*		*Anthophora abrupta* (6) *A.meadii*		*Myzinum quinquecintum* (15) *A.verticillata*	
	Ext	Ins	Ext	Ins	Ext	Ins	Ext	Ins
Mouth Parts	0	0	0	0	4	0	6	3
Claws								
front	130	105	0	0	0	0	2	1
middle	46	37	0	0	0	0	4	1
hind	26	20	0	0	0	0	2	0
Pulvilli								
front	0	0	0	0	0	0	114	74
middle	0	0	0	0	8	3	54	38
hind	0	0	0	0	12	8	16	14
Tarsi								
front	20	17	0	0	0	0	98	32
middle	66	46	56	42	0	0	206	82
hind	78	57	36	18	0	0	132	92
Tibiae								
front	0	0	0	0	0	0	8	1
middle	4	2	0	0	0	0	0	0
hind	14	4	6	3	0	0	12	3
Thorax	0	0	0	0	2	0	0	0
Totals	384	288	98	63	26	11	654	341
% Transferred	(75.0)		(64.3)		(42.3)		(52.1)	

Ext = Extracted; Ins = Inserted; Sample size (in parentheses).

size on this milkweed than those on the other small flowered marsh milkweed (*A. incarnata*). The orders of Diptera, Coleoptera, and Hemiptera were also represented in collections taken from the flowers, but none of the specimens carried significant numbers of pollinia or had sufficient numbers of pollinial sacs missing as an indication of effective pollination. The largest numbers of pollinia for these species were attached to the tarsal hairs of the insects (Table 5). The average numbers of pollinia carried were much fewer, and the percentages of insertion were also lower for all insects visiting this species as compared to the insects visiting *A. incarnata*.

Many insects collected from *A. verticillata* carried pollinia from *A. incarnata* and/or *A. syriaca* (Table 7). More than half of the specimens of *Sphex ichneumoneus* carried the pollinia of two or three species of *Asclepias*. Two of the 15 specimens of *Myzinum quinquecintum* collected, were found to have pollinia of *A. incarnata* attached, even though none was observed on or collected from flowering stems of that milkweed.

A. viridiflora (small green milkweed). Only 5 specimens of the bumble bee (*B. griseocollis*) were collected on the 83 flowering stems of this milkweed observed during two blooming seasons (Table 1). Of a total of 176 pollinia sacs extracted, 70 were inserted (39.8%). Most of the pollinia (88.7%) were attached to the tarsal hairs of all three pairs of legs. The greatest number was carried on the middle pair with a lesser number on the tarsal hairs of the third pair of legs. Approximately 10.2% were carried by tibial hairs of the front and middle legs. Only one pollinia was attached to the mouth parts.

DISCUSSION

In this study, over 40,000 flowering stems of twelve species of *Asclepias* were observed for possible insect pollinators. The number of flowering stems were not divided equally among these twelve species. Ninety-four percent of the stems observed belonged to three species: common milkweed (*Asclepias syriaca*), whorled milkweed (*A. verticillata*) and marsh milkweed (*A. incarnata*). These species are the most common of the milkweeds forming large colonies with hundreds or even thousands of flowering stems. Also they are the weediest of the milkweeds, growing in early seral stages of succession. Insect visitors are attracted to them, and large numbers of specimens can be collected from them in relatively short periods of time. They provide abundant data for statistical analysis and are usually the species studied by ecologists.

On the other hand with few exceptions, most of the other species of milkweeds are hardly studied at all. They are rare or of uncommon occurrence and grow as widely scattered single plants or in small colonies. They are usually associated with higher seral stages of ecological succession (prairies, savannas, and open woods) or require unusual soils, such as, sand or calcareous gravels. Moreover, very few insect visitors seem to be attracted to their flowers. Only 4 specimens were taken from *A. hirtella*, 9 specimens from *A. meadii*, 2 from *A. lanuginosa*, and 5 from *A. viridiflora* (Table 1). Pod production in these four species of *Asclepias* is usually very poor (Betz and Lamp 1990).

There is some question as to whether the principal pollinators collected on *Asclepias spp.*, and reported in this paper, are the same ones that were the principal pollinators of *Asclepias* in pre-settlement times. This is especially true for the exotic honey bee (*Apis mellifera*). This is almost the exclusive pollinator of *A. syriaca* today, and it accounts for 99.9% of the pollinial sacs that were inserted in that species. This exotic species also appears to be the major pollinator of *A. purpurascens* (82.5%), *A. tuberosa* (80.8%), and *A. sullivantii* (79.06%), and it is relatively important in the pollination of *A. exaltata* (52.5%), *A. incarnata* (24.5%), and *A. verticillata* (11.0%).

If *Apis mellifera* was not in North America in pre-settlement times, what were the principal pollinators of these *Asclepias* species? One possibility is that some of the present-day pollinators, such as bumblebees (*Bombus*), thread-waisted wasps (*Sphex, Tachytes*), and paper wasps (*Vespidae*), may have existed in greater numbers in pre-settlement times than at present. Thus they could have been major pollinators for these species. There is circumstantial evidence that there has been a major decline in native insect populations since settlement (Betz and Lamp 1990). This decline may have been due to: (1) loss of habitat; and/or (2) heavy competition for nectar from the ubiquitous *Apis mellifera* (Paton 1993).

Another possibility is that there may have been other pollinators of *Asclepias* in presettlement times that were then common or even abundant. These pollinators may have suffered precipitous declines in population and thus are rare today. In some cases the presettlement pollinator or pollinators may have been extirpated entirely from the region. The differences in floral displays among *Asclepias* species, such as colors and sizes of the flowers and the wide variation in umbel types, would tend to support such a hypothesis. For example, in some species, such as *A. lanuginosa* and *A. hirtella*, the flowers are small; whereas, in *A. meadii* and *A. sullivantii*, they are fairly large. Many species have purple or pink flowers, as in *A. syriaca* and *A. purpurascens*; whereas, other species have a variety of colors: green in *A. viridiflora*; orange or yellow in *A. tuberosa*; white in *A. verticillata* and *A. exaltata*; and greenish-yellow in *A. meadii*. In some species the flowers have long pedicels arranged in loose umbels, as found in *A. amplexicaulis* and *A. hirtella*; whereas, in others, as shown by *A. viridiflora* and *A. tuberosa*, the flowers have shorter pedicels and the umbels are tight and upright.

The inflorescence of Mead's milkweed (*A. meadii*) may be an example offering support to the hypothesis of pre-settlement pollinators. This species produces a greenish-yellow, flat, and nodding umbel in which the dozen flowers (mean 12, S.D. 3.3) are tightly packed together and lie in the same plane. When pollinators are on it, sucking nectar and presumably pollinating its flowers, they are partially hanging onto the flowers upside down. Was the evolution of this type of floral inflorescence adapted for a "generalist" pollination syndrome or for a specific pollinator? The present study indicates that the uncommon and even perhaps rare mining bee, *Anthophora abrupta* in the family Anthophoridae, may be a principal pollinator of *A. meadii* instead of the more common bumble bees (*Bombus spp.*) (Table 1). This species is robust and hairy and superficially resembles a small bumble bee worker.

Anthophora abrupta and other related anthophorid bees, may have occupied the ecological niches in presettlement times now occupied by *Apis mellifera*. In comparison to the 12 mm. long *Apis mellifera* worker, the body size for *Anthophora abrupta* is slightly larger. The female *Anthophora abrupta* female is 18 mm long, and the male is 13-16 mm (Mitchell 1962). This larger size would enable it to more easily break pollinial translator arms and thus not become entrapped on *Asclepias* flowers as is often the case with the workers of *Apis mellifera* (Robertson 1927). Moreover, while *Anthophora abrupta* is not social like the honey bee, large numbers nest

Table 7. Insects carrying more than one species of *Asclepias* pollinia.

	Apis mellifera (35)	*Bombus griseocollis* (39)	*Myzinum quinquecinctum* (15)	*Sphex ichneumoneus* (37)	*Sphex pennsylvanicus* (26)
A.v+s+i	3	0	0	8	4
A.v+s	3	4	0	2	0
A.v+i	1	2	2	4	4
A.s+i	1	10	0	7	2
Total with different pollinia	8	16	2	21	10
Percent of total collected	23	41	13	57	39

v = *A. verticillata*; s = *A. syriaca*; and i = *A. incarnata*; Sample size (in parentheses).

together in communal burrows in the ground or in clay banks. Thus this species could be an important pollinator in late spring and early summer during this bee's reproductive season (Rau 1929 and Pearson 1933).

Another similarity between *Anthophora abrupta* and *Apis mellifera* is that during the pollination of milkweeds there is a preponderance of the attachment of the corpuscula and chains of pollinia to the pulvilli (Tables 4 and 6). This is in contrast to the bumblebees (*Bombus*) and *Sphex* wasps where the attachment is to the tarsal hairs (Tables 3 and 5). It is possible that the raised anther wings on *Asclepias* flowers may have evolved to guide more effectively the tarsal claws of presettlement pollinators to enable the pulvilli with their chains of pollinia to be directed along the stigmatic slit. The attachment of corpuscula to other parts of the pollinator, such as tarsal and tibial hairs, and their insertion into the stigmatic chambers may be less efficient and more accidental.

Many genera in the Anthophoridae have been reported as visitors, sometimes frequently, to other species of *Asclepias*. Some were observed carrying pollinia. These were: (1) *Anthophora, Tetralonia* on *A. purpurascens*; (2) *Epeolus, Florilegus, Melissodes* on *A. sullivantii*; (3) *Anthophora, Epeolus, Florilegus, Melissodes, Peponapis, Tetralonia, Triepeolus* and *Xenoglossa* on *A. syriaca*; (4) *Melissodes* on *A. tuberosa*; (5) *Ceratina, Melissodes, Triepeolus* on *A. verticillata*; (6) *Anthedonia* on *A. viridiflous* and (7) *Melissodes* and *Svastra* on *A. incarnata* (Robertson 1927). The anthophorid *Melissodes desponsa* was found to be a major pollinator of *Asclepias quadrifolia* in western Missouri (Chaplin and Walker 1982).

There are a number of factors which hinder studies on possible presettlement pollinators of *Aslcepias* species. On the one hand, with the possible exception of the few common species, such as *A. syriaca* and *A. incarnata*, most populations of less common, even rare, milkweeds are declining (Betz 1989, Betz and Lamp 1990). It is questionable if sufficient numbers of plants could be found for these in relatively undisturbed communities (prairies and savannas) in order to collect statistically reliable data. On the other hand, the populations of potential pollinators are low and also possibly declining (Betz and Lamp 1990). Many of the species of bees listed for the Chicago Region (Pearson 1931), and found in the collections at the Field Museum of Natural History, Chicago, Illinois, have not been collected for decades.

Another problem to contend with is the presence of the ubiquitous honey bee (*Apis mellifera*) which would appear to compete with native bees for nectar (Paton 1992). It is interesting to note that this species is presently being parasitized by two introduced mites: (1) the tracheal mite (*Acarapis woodi*); and (2) the ectoparasitic Varrosa mite (*Varroa jacobsoni*). These are causing wide-spread destruction of *Apis mellifera* colonies and may reduce their numbers sufficiently to allow the return of larger populations of native bees.

In recent times, successful efforts have been made throughout the Middle West to restore and enrich tallgrass prairie remnants (Betz 1986). Rare and uncommon prairie plant species are being grown and reintroduced into these preserves with resulting increases in populations. Unfortunately, almost no efforts have been undertaken to reintroduce the apparently regionally exterminated populations of our native insects into these restored preserves. Hopefully, more attention will be given in the future to the study of the ecological requirements of our native bees so that they can be introduced into prairie and other types of preserves. This could produce ecological communities that would better approximate presettlement communities than those of the present day. This may, in turn lead to the possibility of a better understanding of presettlement pollination ecology.

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LEAFHOPPER EVIDENCE FOR ORIGINS OF NORTHEASTERN RELICT PRAIRIES (INSECTA: HOMOPTERA: *CICADELLIDAE*)

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Abstract. East of Lake Michigan there are 70 grassland sites known to support 37 leafhopper species otherwise associated only with the Great Plains. The presence of monophagous, flightless prairie leafhoppers on Lake Huron islands of known age, and in sites as far east as Ottawa, clearly indicates that a continuous belt of prairie grasses extended from the prairies to south of Ontario before deglaciation; this retreated to Lake Huron islands before 9000 years ago. At least 16 northern prairie leafhopper species are probably associated with this periglacial grassland. Other relict grasslands have 14 species characteristic of the central prairies and are probably of Hypsithermal origin (8000-6000 years ago). Another 7 species in the most southerly grasslands are not restricted to prairies but occur as well in eastern glades; these "prairie peninsula" grasslands probably became established over the last 5000 years.

INTRODUCTION

The Great Plains of North America in prehistorical times tapered eastwards, becoming a mosaic of oak forests and patchy grasslands in Illinois and western Indiana (Figure 1, hatched area). A "prairie peninsula" of isolated grasslands is known to have extended through southern Michigan at least as far eastwards as Columbus, Ohio (Transeau 1935) although now virtually eliminated by agriculture. In Ontario the Ojibway Prairie in Windsor and prairie patches on Walpole Island are considered as part of the "prairie peninsula". Chapman and Pleznac (1982) list 32 "prairie peninsula" sites in Michigan, mainly in the southwest. These "prairie peninsula" sites may be relict patches of a prairie that once was much more extensive, possibly dating from about 8000-6000 B.P. (before the present), a period called the Hypsithermal when summer temperatures were 1° to 2°C higher than today (Anderson et al. 1989).

The Hypsithermal had little effect east of southernmost Ontario, only causing an increase in white pine stands (Anderson 1985). There were once extensive oak-savannah grasslands from Long Point north to Kitchener, Ont., but these appeared between 6000 and 4000 B.P. and apparently are not the result of heightened temperatures. Instead, they are associated with well-drained soils where vegetation is susceptible to fire (Szeicz & MacDonald 1991), presumably lightning-strike fires. An extensive area north of Cobourg, Ont. called the "Rice Lake Plains" appears to be an oak-savannah maintained by Indian activities involving deliberately set fires (Catling et al. 1992).

Many other native grassland patches to the north and east of the "prairie peninsula" have prairie-like vegetation. Sand ridges throughout the northeast may support prairie-like stands of grasses, forbs and creeping juniper, *Juniperus horizontalis*. Catling et al. (1975) record numerous prairie plants from alvar grasslands (associated with thin, readily drying soil over limestone outcrop) in Ontario. But are any of these relict prairies?

Botanical evidence on this question is conflicting. The presence of suites of prairie-adapted plants in modern grasslands supports the idea of a relict prairie. On the other hand, such communities may be due more to microenvironment than to prehistorical vegetational patterns, as most seeds are very easily transported by wind and other means. Some grasses associated with prairies (e.g. prairie dropseed, *Sporobolus heterolepis*) are usually found along watercourses (Dore & McNeill 1980) and may have been spread by water-transported seeds. Larger seeds are often dispersed by animals. Birds, for example, are well-known carriers of many kinds of seeds and have been implicated in seed transferral over thousands of kilometers (Gibbons 1991).

Palynological data (fossil pollen) tells little about grasslands. Grass genera cannot be distinguished, and pollen grain counts are weighted in favour of tree pollen. Pine pollen, for example, can drift hundreds of kilometers beyond the tree line. Discontinuous prairie vegetation may show as little as 10% herb pollen and much smaller levels of grass pollen (Bernabo and Webb 1977).

Palynology suggests that the vegetation of the Great Lakes region cycled rapidly from subarctic, to closed boreal forest, to modern closed mesic forests, without conditions ever suitable for open prairie (Gilliam et al. 1967, Anderson 1989). However, following deglaciation there may have been a period, too brief to show on pollen cores, in which prairie-like grasslands flourished. Alternatively, an open spruce forest could have replaced the treeless flora that initially colonized deglaciated land. Strong evidence for such a mosaic is found in western Canada, where large amounts of *Artemisia* pollen and significant levels of grass pollen coexisted with dominant spruce pollen ca. 10,500 B.P. (Ritchie 1976).

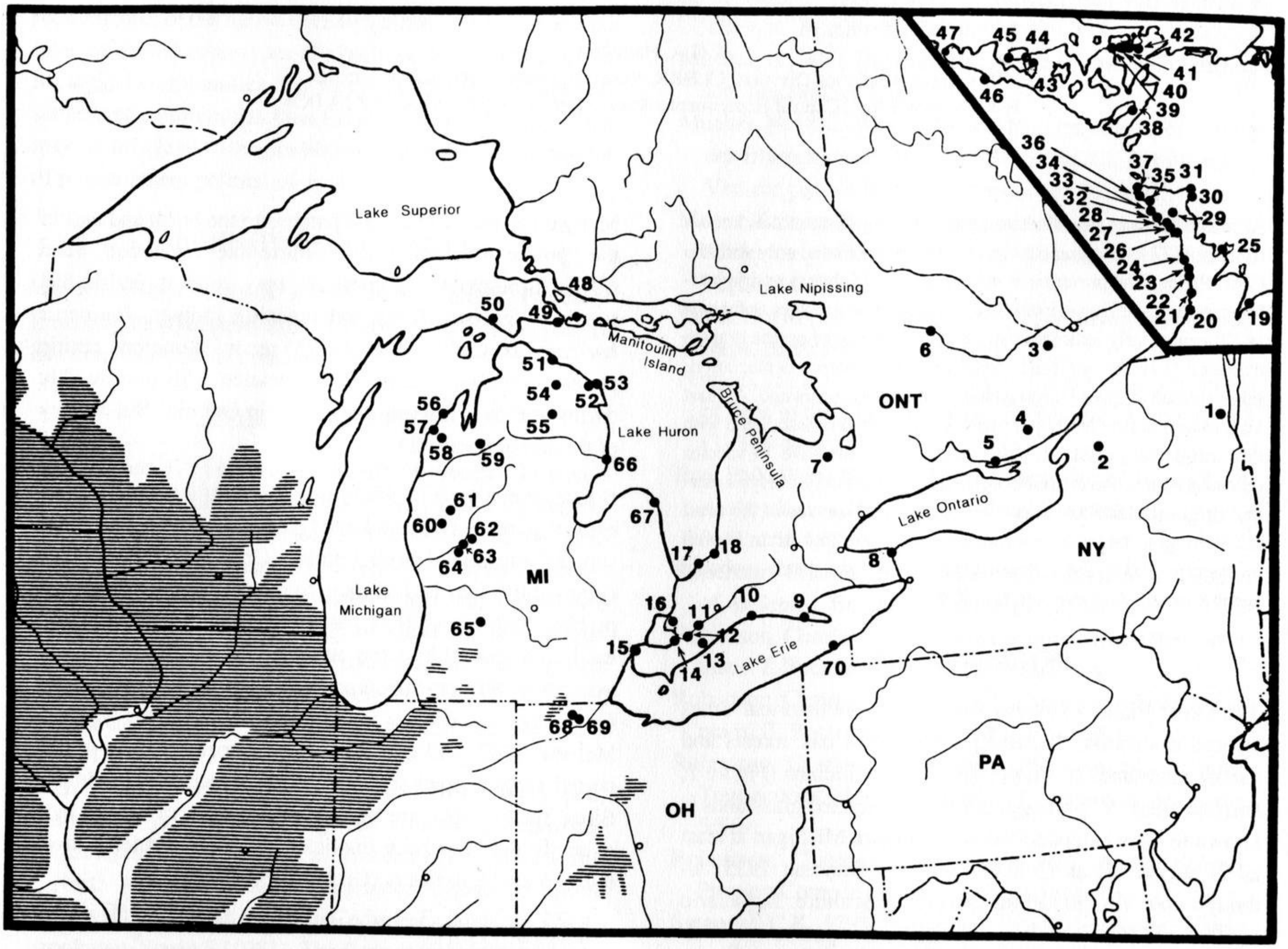


Figure 1. Natural grasslands north and east of true prairie (hatched) in New York state (1-2), Ontario (3-47), Michigan (48-67), Ohio (68-69) and Pennsylvania (70); location not precisely known indicated by an asterisk (*). Inset: Bruce Peninsula, Manitoulin I and adjacent islands of Lake Huron. 1, Elizabethtown; 2, 2 km NW Harrisville, NY; 3, Ramsay alvar; 4, 5 km E Camden East; 5, Point Anne; 6, 5 km E Madawaska, Ont.; 7, 3 km E Sunnidale Corners; 8, *Queenston; 9, Long Point; 10, Port Bruce; 11, *Thamesville; 12, *Chatham; 13, 4 km NE Blenheim; 14, St. Clair Ntl. Wildlife Refuge; 15, Ojibway Prairie; 16, Walpole Island; 17, Ipperwash Beach; 18, Pinery Prov. Park; 19, Squaw Point; 20, Sauble Beach; 21, Oliphant; 22, Red Bay; 23, St. Jean Point; 24, Pike Bay; 25, Prairie Point; 26, Stokes Bay; 27, Pleasant Harbour; 28, 1 km E Pine Tree Harbour; 29, 7 km NE Miller Lake; 30, 3 km SW Cabot Head lighthouse; 31, Cabot Head; 32, Johnston Harbour; 33, 15 km SE Tobermory; 34, 14 km SE Tobermory; 35, Dorcas Bay; 36, 1 km N Baptiste Harbour; 37, Cape Hurd; 38, 19 km SW Wikwemikong; 39, Goat Island; 40, Great La Cloche Island, 5 km E Little Current; 41, same, 8 km further E; 42, Little La Cloche Island; 43, 7 km NE Evansville; 44, 10 km W Gore Bay; 45, W extremity of Barrie Island; 46, Burnt Island; 47, Mississagi lighthouse; 48, Maxton Plains alvar; 49, DeTour Beach; 50, 5 km E Epoufette Bay; 51, 10 km N Huron Beach; 52, North Point alvar; 53, Lighthouse Point; 54, 4 km NW Millersburg; 55, 1 km N Clear Lake St. Pk.; 56, 7 km S Glen Haven; 57, 14 km S Empire; 58, Honor; 59, 5 km W Fife Lake; 60, 2 km S Lilley; 61, 1 km W Idlewild; 62, 4 km W Oxbow; 63, 5 km W Croton; 64, 9 km ESE Newaygo; 65, Middleville; 66, Oscoda; 67, 3 km N Harbor Beach; 68, Irwin Prairie St. Nat. Preserve; 69, Oak Openings St. Nat. Preserve; 70, Presque Isle sand bar.

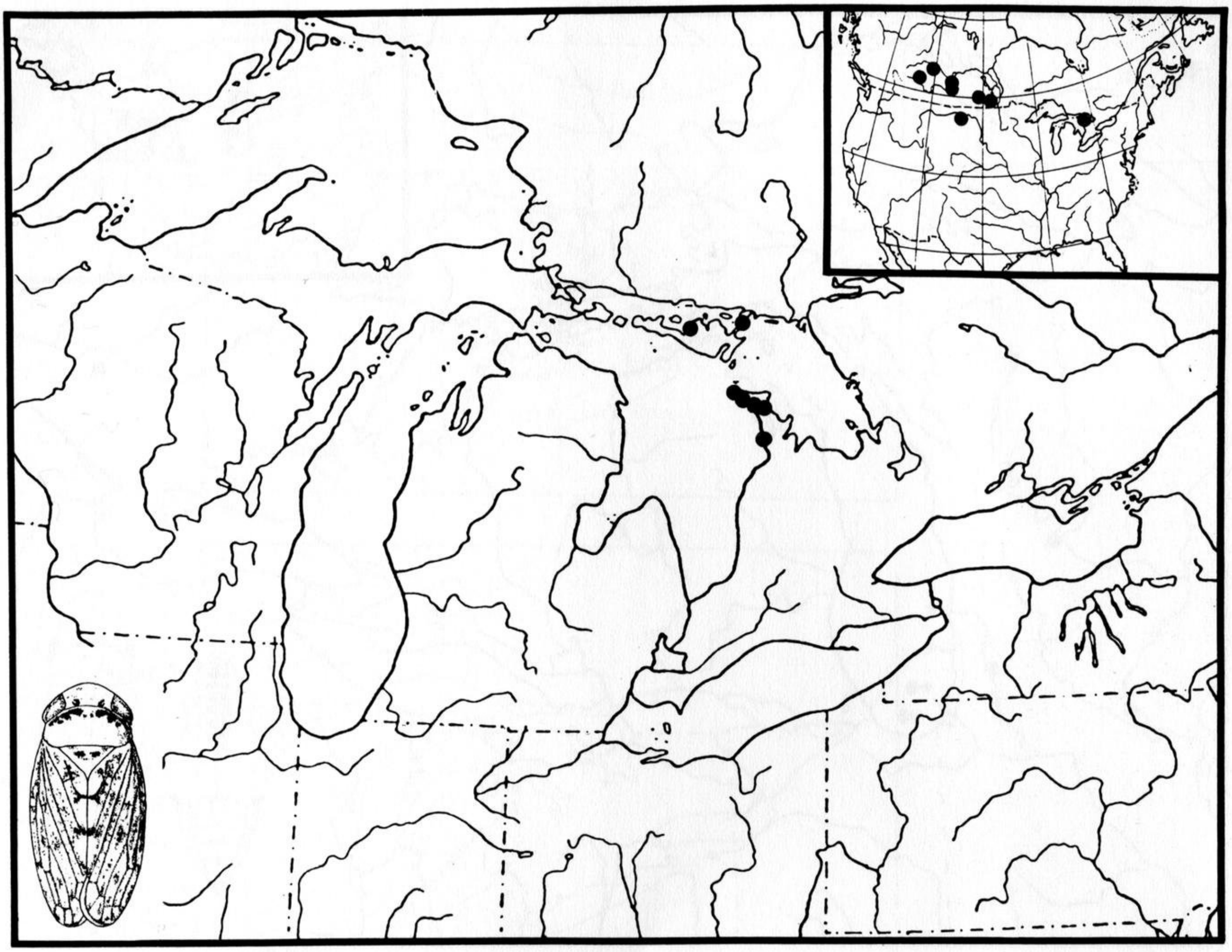


Figure 2. Distribution of *Texananus marmor* (Sanders & DeLong) in the Great Lakes region. Inset: total distribution.

Fossil beetle specimens found in an Illinois site at 21,500 B.P. (representing glacial advance) and in Iowa, Minnesota and Wisconsin sites between 15,000 and 12,000 B.P (representing glacial retreat) show unique faunas unlike either closed spruce forest or tundralike conditions usually associated with glacial-age vegetation (Schwert 1992). These anomalous beetle faunas include 4 species now restricted to western mountains, and 1 species now characteristic of the Great Plains. The species in question suggest the presence of coldwater streams and dry summer conditions followed by early, heavy snowfalls (H. Goulet, personal communication). This would favour spruce forests along streams, with prairie on higher ground produced by summer drought.

Clearly, much additional information is needed to bring the disparate data into agreement. The present study adds data from the distribution of leafhoppers, the insect family Cicadellidae (see representative leafhoppers on Figures 2-3). Comparison of the leafhopper faunas of native grassland areas around the Great Lakes and further eastward helps to characterize these grasslands more completely, and to draw inferences about their origins and persistence. For this task, a detailed account is needed of what we now know about the changes in geography and ecology of the Great Lakes region during the postglacial (Holocene) period.

Historical summary

Lewis and Anderson (1989) presented an analysis of changing lake levels and outflow routes for the Great Lakes in postglacial times. Bernabo and Webb (1977) summarized palynological data for the region over the same period. The following is an integrated summary of their conclusions.

Michigan and southern Ontario were completely deglaciated by 11,200 B.P. At that time, waters from Lake Algonquin (now Lakes Huron and Michigan) flowed across the path now followed roughly by the Trent-Severn canal (between sites 7 and 5 on Figure 1), emptying into early Lake Ontario near present-day Belleville. By 10,800 B.P. this spillway had

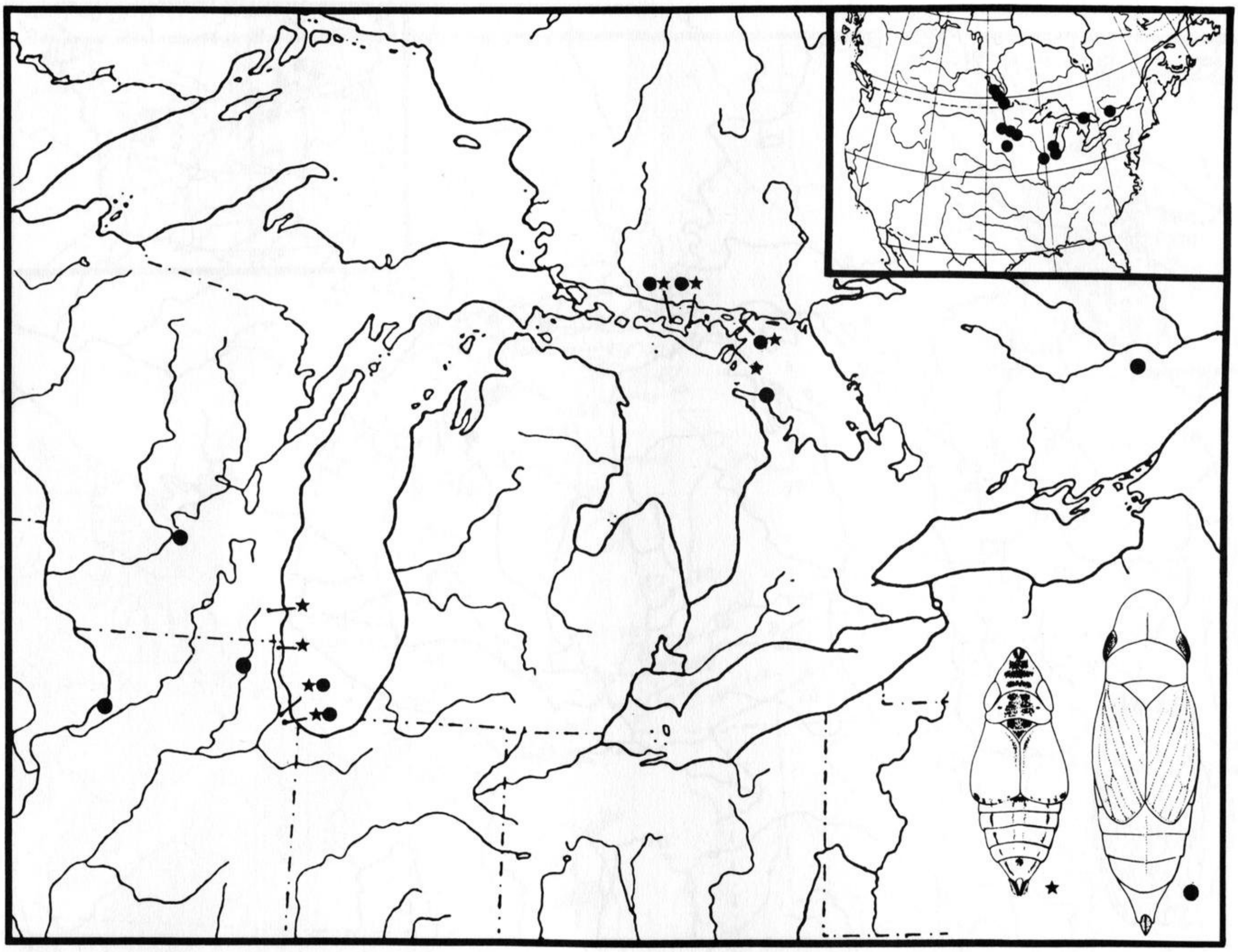


Figure 3. Distributions of *Aflexia rubranura* DeLong (star) and *Memnonia sp.* (= *Hecalus grandis* DeLong nec Shaw) (dot). Inset: total distributions of both species.

risen through isostatic rebound so much that upper Michigan, Manitoulin Island and the Bruce Peninsula were nearly entirely submerged.

Floral evidence for this period suggests a high boreal climate for the vicinity of the lakes. Any mountain tops emergent above the waters would probably have been subarctic and unsuitable for leafhopper survival.

By 10,000 B.P., retreating ice fronts uncovered the Ottawa valley, releasing torrential outflows of Great Lakes water *via* the isostatically depressed proto-lake Nipissing to the Ottawa River (Figure 4). This dramatically dropped the lake level.

Lowered lake levels left a land connection between the Bruce Peninsula and Manitoulin Island (Figure 4) which persisted until 9000 B.P. except for the brief Early Mattawa flood stage (9600 B.P.). During this period, all glacial melt waters from the Great Lakes poured across the La Cloche Islands north of Manitoulin Island, stripping off the topsoil and laying waste to whatever had managed to establish itself there.

While Manitoulin Island was still connected to the Bruce Peninsula the dominant vegetation of this area was spruce forest. It would probably be incorrect to state that it was therefore boreal forest. World temperatures were already elevated at least to modern levels and partial grassland vegetation (indicated by 10% herb pollen levels) had established themselves in southern Ontario. Trees, growing under poor soil conditions, were probably migrating northwards more slowly than temperature alone would dictate (for data from eastern Canada, see Hamilton & Langor 1987, Table 9).

By 9000 B.P. lakewater outflow was diverted across the ridge connecting Manitoulin Island to the Bruce Peninsula. For 400 years there was a period of possibly fluctuating lake levels. By 8600 B.P., Manitoulin became continuously connected to the north shore by isostatic emergence of the vicinity that now includes the La Cloche Islands (Figure 5). This northern

Figure 4

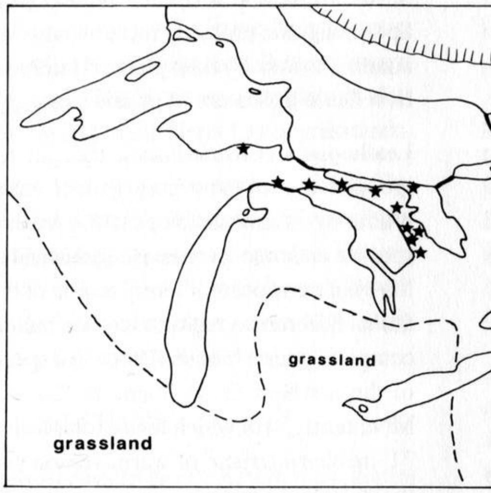


Figure 5

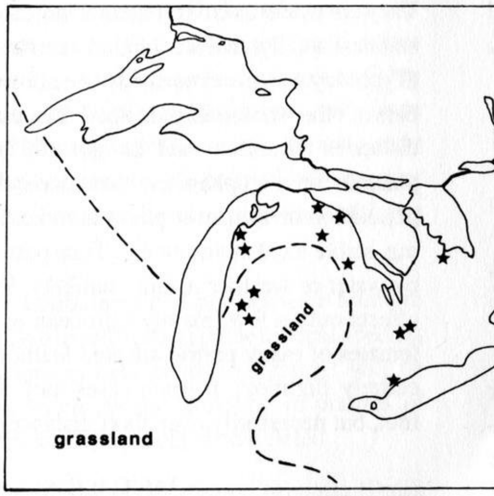
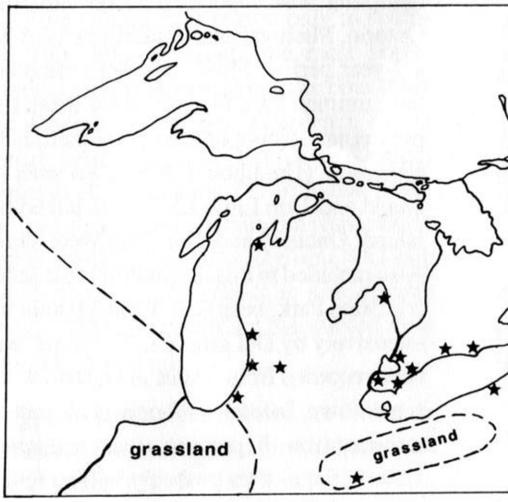


Figure 6



Figures 4-6. Inferred water level of Great Lakes and 10% herb pollen isobar (dotted line). 4, ca. 9000 B.P. (redrawn from Lewis and Anderson 1989, fig. 8e) and periglacial grassland sites (stars); 5, ca. 8000 B.P. (redrawn from Lewis and Anderson 1989, fig. 8g) and Hypsithermal prairie sites (stars); 6, ca. 4000 B.P. (redrawn from Lewis and Anderson 1989, fig. 8h) and "prairie peninsula" sites (stars).

connection lasted until 7800 B.P. when present-day channels formed. The channel between Goat Island and Manitoulin Island is deep enough to have been stable from that time.

From 8000-6000 B.P. temperatures were at their postglacial maximum. Grasslands established themselves in southern Michigan and adjacent Ontario by about 8000 B.P. By 7000 B.P. grasslands had retreated from southern Ontario but still occupied much of western and central Michigan. Pine forests were dominant on Manitoulin by 8000 B.P. but oak probably never came in significant levels even to the Bruce Peninsula.

Isostatic rebound continued slowly until the Nipissing channel came to the same level as the St. Clair River about 4700 B.P. About this time, and possibly as a result of the establishment of the St. Clair River, Lake Erie rose to its present level (Figure 6). This probably profoundly influenced the incidence of thunderstorms in its vicinity, as fire-induced "prairie peninsula" in Ontario and Ohio dates from about this time.

Prairie insects

Published entomological evidence for insects unique to modern prairies is scanty at present. A single prairie skipper, the Garita skipperling *Oarisma garita* (Reakirt) has been reported from the La Cloche Islands (Catling 1977) but this might possibly be either wind-transported or accidentally introduced by man.

True bugs (Rhynchota) are frequently host-specific. Their intimate association with characteristic habitats, their dependence on their host plants and their ability to survive in small sites makes them good indicators of prehistorical vegetation patterns. Within Rhynchota, only certain Homoptera are intimately associated with prairie plants. These include:

Plant hoppers (*Fulgoroidea*): mainly tropical, these insects prefer forest environments. Calisceline Fulgoroidea, by contrast, are associated with temperate-zone grasslands. Five such species find their northeastern limits near the Great Lakes. All are widespread in glades and clearings throughout the southern U.S.A. and are not restricted to prairie sites.

Spittlebugs (*Cercopidae*): 3 of the 4 species associated with prairies are found in Great Lakes grasslands. *Philaenarcys killa* Hamilton of central and southern Michigan and adjacent Ontario ranges westward to Minnesota and south to Oklahoma. The closely related *P. bilineata* (Say) which is abundant on the northern plains is also found on little bluestem, *Schizachyrium scoparium* at the same Lake Huron site as the Garita skipperling; but it is also widely distributed through the boreal zone on bluejoint, *Calamagrostis canadensis*. The third spittlebug, *Lepyronia gibbosa* Ball occurs from Manitoba to Texas, and is also known from the Newaygo plains of Michigan, and several sites near Boston, Massachusetts. Spittlebugs are probably more heavily influenced by climatic conditions than by host plants (Hamilton 1982) and may not be reliable indicators of prairie sites.

Leafhoppers (*Cicadellidae*): thought to be the only insect group that evolved whole genera within North American prairie environments (Ross 1970), leafhoppers have over 600 species endemic to western grasslands in North America. Many of these occur in every region of the prairies, with great faunal differences region to region indicating an ancient, and complex, prairie biome. About 110 species are characteristic of the northern Great Plains in Canada east of the Rocky Mountains, 70 of which feed exclusively on grasses. Another 71 are characteristic of warm-season grasses on the prairies in the United States.

They are useful as environmental indicators because only the smallest and lightest are regularly carried by wind, and these (Typhlocybinae) are mostly tree-feeding species. Most members of other subfamilies do not disperse rapidly or over great distances (Hamilton and Langor 1987). Many are monophagous or oligophagous; their dependance on a sizeable population of their host plants is indicative of a long-standing, stable local environment. Transportation of such insects by water or weather is quite unlikely. Even human activity affects only a few, mainly European species. Furthermore, females of many prairie-adapted leafhoppers are usually or entirely flightless. In such cases they disperse actively on foot, but necessarily over short distances each year.

METHODS

Sampling was conducted in 66 sites throughout southern Ontario, Michigan and adjacent parts of New York state over a 2-year period. Most sites were sampled in both early and late summer. Exact localities for these sites, together with a preliminary listing of their homopterous faunas, is presented elsewhere (Hamilton 1990). Two sites on and near Barrie Island and 1 on Little La Cloche Island (all near Manitoulin Island, Ontario) and 2 in Ohio were sampled subsequently. Also included in this discussion is the sandbar site of Presque Isle State Park, near Erie, Pennsylvania which was collected intensively by DeLong (1923). Prairie leafhoppers have also been recorded from 3 sites in Ontario whose precise location is unknown. In total, leafhoppers characteristic of prairies are recorded from 70 prairies, alvars and sandy localities (Figure 1). Additional sites probably will be found in Ohio, where 2 prairie leafhoppers monophagous on sideoats grama, *Bouteloua curtipendula* have been found (Whitcomb & Hicks 1988 and personal communication).

These samples were compared to conserved prairie localities in Minnesota, North Dakota and Manitoba and 3 coastal sites in southwestern Michigan adjacent to the eastern tip of the true prairie. Additional grassland sites near the Atlantic coast of Maryland, Pennsylvania, Nova Scotia and Prince Edward Island were also compared. The latter are faunistically dissimilar to both full prairie and to the Great Lakes grasslands.

Many of the sites were less than a hectare in extent. The vulnerability of these sites is vividly illustrated by a northern site of the leafhopper *Dorydiella kansana* Beamer in Ontario (Squaw Point, north of Owen Sound), which was "developed" as housing lots with complete devastation of the flora the year after I had sampled there (1988).

RESULTS

Most native grasslands in eastern North America are glades or clearings in woodlands and have only widespread leafhoppers characteristic of understory and disturbed sites. By contrast, many eastern prairie sites, alvars and sand ridges have 1-14 leafhopper species characteristic of prairies (Map 1). Remarkably, many of the Great Lakes sites with large numbers of prairie leafhopper species are alvars and sandy areas rather than deep-soil prairie. No prairie leafhoppers at all have been found in deep-soil prairie sites east of Long Point, Ontario.

A total of 45 species characteristic of prairies were found in 70 Great Lakes sites. An identification guide to these species, together with their known host plants and ranges will be presented elsewhere when current sampling in prairies of Michigan, Wisconsin and Minnesota is completed.

Three prairie leafhopper species, *Flexamia areolata* (Ball), *Orocastus perpusillus* (Ball & DeLong) and *Polyamia saxosa* DeLong enter the Great Lakes region only in southernmost Michigan. This area represents the most northeastern extent of continuous presettlement prairie. Four other leafhopper species feeding on sedges, *Limotettix bisoni* Knull, *L. parallelus* sensu Medler nec Van Duzee, *Paraphlepsius continuus* (DeLong) and *P. turpiculus* (Ball) range into northern forest areas and are thus not restricted to prairie sites. One other species, *Balclutha neglecta* (DeLong & Davidson) is wind-dispersed and occurs in sites remote from its breeding areas. These 8 species are discounted from the subsequent listings and analysis.

The remaining 37 prairie leafhopper species are found in eastern North America only on native grasslands adjacent to, or east of the Great Lakes (Table I). These occur most frequently in Ontario at Ojibway Prairie (Figure 1, site 15), Ipperwash Beach (site 17), and on the La Cloche Islands north of Manitoulin Island (sites 39-42). In Michigan the best sites are Maxton Plains on Drummond Island (48), North Point (52-53), and Newaygo Plains (62-64).

Table I. Prairie leafhoppers by sites (sites numbered as in Figure 1).

LEAFHOPPERS OF NORTHERN GRASSLANDS	
Aceratagallia n. sp.:	2, 4, 5, 25, 29, 39, 41, 44, 48, 61, 63
Aflexia rubranura (DeLong):	38-42, 44-45
Athysanella terebrans Gillette & Baker:	17
Auridius helvus (DeLong):	62-64
Auridius n. sp.:	6, 31, 40, 48, 50
Commellus sexvittatus (Van Duzee):	50, 58
Extrusanus n. sp.:	62-64
Flexamia delongi Ross & Cooley:	17-18, 22-24, 26-28, 32-33, 35, 37, 39-42, 48-49, 52, 53-54, 61-62, 64, 69
Flexamia inflata (Osborn & Ball):	4-5, 15
Limotettix n. sp. A:	24, 51
Memnonia grandis (DeLong nec Shaw):	3, 31, 40-42, 44-45
Mocuellus americanus Emeljanov:	39-42
Paraphlepsius umbrosus (Sanders & DeLong):	17, 20
Psammotettix knullae Greene:	58
Texananus arctostaphylae (Ball):	3, 17, 23, 30, 48, 50, 54-55
Texananus marmor (Sanders & DeLong):	23, 29, 32, 34-36, 42-43
LEAFHOPPERS OF SOUTHWESTERN GRASSLANDS	
Commellus comma (Van Duzee):	1, 60, 63-64
Dorydiella kansana Beamer:	13, 15, 17, 19, 25, 52, 68, 70
Flexamia prairiana DeLong:	15, 17
Graminella mohri DeLong:	30, 57, 70
Graminella oquaka DeLong:	14-16
Graminella pallidula (Osborn):	8, 10, 15, 67, 70
Laevicephalus minimus (Osborn & Ball):	5
Laevicephalus unicoloratus (Gillette & Baker):	7, 15, 20, 39-42, 44, 52, 54, 56, 59, 61-62, 64, 68
Limotettix n. sp. B:	52, 67
Macropsis quadrimaculata Breakey:	51, 53, 55, 66
Paraphlepsius lobatus (Osborn):	17-18, 24, 26, 28, 32-33, 35, 39, 48, 52-54
Polyamia caperata (Ball):	22, 52, 56, 65
Polyamia compacta (Osborn & Ball):	35
Stirellus bicolor (Van Duzee):	65
LEAFHOPPERS OF SOUTHEASTERN GRASSLANDS	
Balclutha abdominalis (Van Duzee):	14-16
Chlorotettix fallax Sanders & DeLong:	15
Chlorotettix spatulatus Osborn & Ball:	15, 17-18, 21-22, 24, 70
Flexamia reflexa (Osborn & Ball):	17
Hecalus flavidus (Signoret):	15
Mesamia nigridorsum (Ball):	8, 11-12, 15, 64, 69
Xerophloea major Baker:	15

The faunas of the grassland sites studied fall into 3 main groups:

1: Deep-soil "prairie peninsula" prairies in Ontario (west of London) to Michigan (principally in the southwest), and alvars and glades around Lake Erie and Lake Ontario (Figure 6) have 7 southern leafhopper species, 6 of which occur in

Ojibway Prairie. These leafhoppers are not restricted to arid sites. Their ranges may include southern grasslands, and glades or clearings along the Ohio River system and on the coastal plain of the eastern USA (Whitcomb & Hicks 1988, figures 29, 41, 43, 47-48, 51). Their distribution is similar to that of Calisceline Fulgoroidea, mentioned above.

2: Alvars and sandy areas in central Michigan and along the southern shores of Lake Huron (Figure 5) have leafhoppers dominantly of central prairie origin. Fourteen leafhopper species found in various grasslands are probably of Hypsithermal origin. Most sites have only a few such species. The most number of western leafhoppers from any 1 site are 4 each from North Point, Ojibway Prairie and Ipperwash Beach.

3: Alvars and sandy areas in northern Michigan, around Manitoulin Island and the Bruce Peninsula, and an alvar near Ottawa (Figure 4) have leafhoppers mostly characteristic of Canadian prairies. Sixteen western leafhopper species are associated with such grasslands; 7 of these occur on the La Cloche Islands.

DISCUSSION

Many of the leafhoppers found in the "prairie peninsula" of southern Ontario and adjacent Michigan are northernmost records of widely distributed southern species. They probably represent geologically recent immigrants. By contrast, most of the other leafhoppers found in the Great Lakes region that are characteristic of prairies show range disjunctions to greater or lesser degree. These distributions suggest that their ranges were once more extensive and have since contracted. Those from central Michigan usually show disjunctions with more westerly or southwesterly prairie ranges. This suggests an Hypsithermal origin for these faunas. In more northerly and eastern sites, most prairie leafhoppers present even greater range disjunctions with species now usually characteristic of northern prairies, suggesting a very early postglacial origin.

Large, heavy-bodied monophagous leafhoppers are least likely to be wind transported. One such is *Texananus marmor* (Sanders & DeLong), which feeds only on creeping juniper. Known otherwise only from the northern Great Plains, it is common throughout the Bruce Peninsula in Lake Huron and occurs sparsely on Manitoulin Island and adjacent Little La Cloche Island (Figure 2). Although its host is abundant in Michigan it has never been taken there. Evidently it migrated from the Bruce Peninsula north to Manitoulin Island, probably when the 2 were joined by a land bridge, but was unable to enter Michigan due to persistent water channels between Manitoulin and the offshore islands of Michigan.

Leafhoppers with wingless females disperse still more slowly, and wind could carry them over only small water bodies such as rivers. There are 2 leafhopper species on prairie dropseed (*Sporobolus heterolepis*): an undescribed species of *Memnonia*, previously reported as *Parabolocratus grandis* Shaw (DeLong 1948) with flightless females, and the red-tailed leafhopper, *Aflexia rubranura* (DeLong) which is wingless in both sexes. The *Memnonia* is found from Manitoba to northern Illinois, on Manitoulin I, on the Bruce Peninsula and at Ramsay alvar (Figure 3, dot) near Ottawa, Ont. *Aflexia rubranura* is much more patchy in its distribution, in Ontario occurring only on and around Manitoulin Island (Figure 3, star).

The wingless leafhoppers *Memnonia* and *Aflexia* were absent from Manitoulin Island and adjacent Barrie and La Cloche Islands until glacial waters subsided 10,000 years ago (or more probably after the Early Mattawa Flood, 9600 B.P.). That both species (lacking females that can fly) are now found on land separated by extensive water bodies means their present distributions are attributable to postglacial geological changes. Similarly, the heavy-bodied *Texananus marmor* probably dispersed across these islands at the same time.

The establishment of a land connection to the Bruce Peninsula from 10,000-9000 B.P. permitted *Texananus, Aflexia* and *Memnonia* to invade the island. Similarly, La Cloche Islands were inundated until 9000 B.P., and subsequently could have acquired wingless leafhoppers from Manitoulin Island until the northern channel formed about 7800 B.P. During this time no palynological evidence exists for continuous prairie in the vicinity of Manitoulin and the Bruce Peninsula. Yet it must have been there, for how else would wingless prairie insects come to islands cut off from southern and western invasions by broad water channels existing continuously for 9000 years? An open spruce forest, such as that indicated by fossil beetle records discussed above, seems the answer. Even patchy grasslands, if in constant flux, would permit wingless insects an invasion route.

Could wingless leafhoppers have migrated quickly enough to take advantage of such shifting grassland patches? Their presence in every patch of prairie dropseed throughout Manitoulin Island and its offshore islands, despite the great distances now existing between these patches, suggests that these insects are indeed rapid walkers. Therefore a rate of 300 km (southern Ontario to La Cloche Islands) in roughly 1000-2000 years would not be unreasonable provided that the host plant was found extensively at the time of migration. This is probable as deep soils would not have accumulated extensively. It is clearly not possible for these insects to have migrated all the way to the La Cloche Islands from Illinois, crossing major river drainage systems, in the same time interval. Hence, their presence in a periglacial grassland of great east-west extent is a necessary presupposition.

CONCLUSIONS

Leafhoppers thus give compelling evidence for 3 generations of native grasslands in the region of the Great Lakes.

Oldest of these was a periglacial grassland in open spruce forests from the interface between ice-induced tundra to the north and closed spruce forests to the south. Fragments of this grassland retreated northwards as postglacial temperatures ameliorated, ca. 9000 B.P., leaving characteristic western flora and leafhoppers on prairies from Illinois to Manitoba, on alvars and sand ridges around the northern Great Lakes, and at least as far east as Ottawa (Figure 4). Possibly the prairie spittlebug sites in Massachusetts represent the eastern extremity of this grassland.

Hypsithermal grasslands ca. 8000-6000 B.P. probably were best developed in sandhills of central Michigan (Figure 5). Their present disjunct distribution is a reflection of deteriorating world temperatures since then.

The "prairie peninsula" (Figure 6) developed after 6000 B.P. only where soils are very well-drained and fires fairly frequent. Hence, these grasslands were probably always isolated from each other.

ADDENDUM

Collecting in 1993 disclosed the presence of *Laevicephalus minimus* (Osborn and Ball) along the Grand River at Brantford Golf Club, Ontario.

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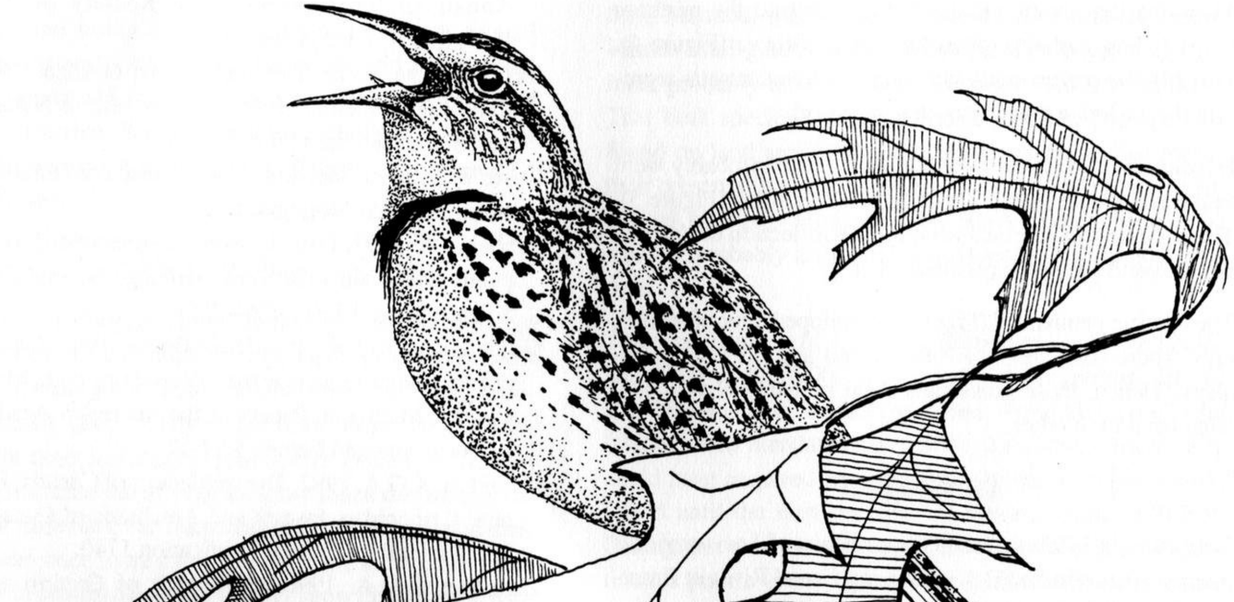

HIBERNATION AND LIFE HISTORY OF THE FRANKLIN'S GROUND SQUIRREL (*SPERMOPHILUS FRANKLINII*) IN A RESTORED PRAIRIE

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Abstract. The emergence patterns of the Franklin's ground squirrel *(Spermophilus franklinii)* were studied for five years in a restored prairie on the Knox College Biological Field Station in west-central Illinois. The earliest emergence recorded was 16 May. The onset of hibernation in adult males and females occurred in late August while juveniles immerged as late as October 25. These data contrast with those of other studies (Murie 1973, Iverson and Turner 1972, Choromansky-Norris et al. 1986) which show that emergence and immergence occur up to one month earlier in Manitoba and North Dakota populations. One selective advantage of late emergence in Illinois may be the avoidance of late winter storms and cold weather. A second is that Franklin's ground squirrels show a strong preference for dense cover which does not develop on these prairies until May. An analysis of the patterns of weight gain indicates the Franklin's ground squirrels in Illinois hibernate at weights similar to those of more northern populations.

INTRODUCTION

The Franklin's ground squirrel (*Spermophilus franklinii*) was introduced to the Knox College Biological Field Station in 1969 as part of a prairie restoration project. Subsequent to its release on the station, studies of the success of the introduction (VanPetten and Schramm 1972) and of home range and habitat use (Krohne et al. 1973) were undertaken. These studies showed that the Franklin's ground squirrel has a strong preference for tallgrass prairie habitats.

During the course of these previous studies, considerable data were gathered on the phenology of this species in west-central Illinois. These data form the basis of a comparison with previous studies of the species in other parts of the range (Sowls 1948, Iverson and Turner 1972, Murie 1973, Choromanski-Norris et al. 1986 and Benjamin 1991).

Hibernating ground squirrels (genus *Spermophilus*, family Sciuridae) face the daunting task of emerging from the hibernaculum, finding mates and breeding, raising a litter and accumulating sufficient fat reserves to survive hibernation, all in a few months. Consequently, the phenology of life history events has been of considerable interest in this genus and a large literature documents the patterns throughout North America. In general, emergence from hibernation is delayed at high latitude or altitude. The latitudinal trend has been documented in the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*) (Rognstadt 1965, Criddle 1939, McCarley 1966, Wade 1950), and Richardson's ground squirrel (*S. richardsoni*) (Michener 1977, Clark 1970, Nellis 1969). Delayed emergence at higher elevations has been reported in the golden-mantled ground squirrel (*S. lateralis*) (Bronson 1977), the Columbian ground squirrel (*S. columbianus*) (Adams 1961) and Belding's ground squirrel (*S. beldingi*) (P. Sherman, personal communication). This paper documents an apparent exception to these patterns.

METHODS

The study was conducted on the Knox College Biological Field Station located 7.2 km south of Victoria, Knox Co., Illinois. The primary study area was a 20 ha restored prairie dominated by big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*) and little bluestem (*Andropogon scoparius*). Dominant forbs include compass plant (*Sylphium laciniatum*), prairie dock (*S. terebinthinacium*), goldenrods (*Solidago spp.*) and rattlesnake master (*Eryngium yuccifolium*). These species represent some of the dominant species present in prairie habitats prior to settlement. Previous studies indicated that Franklin's ground squirrels preferentially use prairie habitats on the field station (Krohne et al. 1973).

The source colony for the 1969 introduction was a native population inhabiting a railroad right-of-way located 15 km south of the field station near Dahinda, Knox Co., Illinois. The introduction produced a stable, reproducing colony averaging 38.2 individuals (VanPetten and Schramm 1972).

A large, irregular trapping grid consisting of 46 stations 65 m apart was established in the grasslands with additional lines or stations as needed to capture particular individuals. Two 20 cm x 20 cm x 60 cm Havahart traps, baited with sunflower seeds and corn were placed at each station. These were modified by placing a wire under the front edge of the treadle so that the trap would not close until a squirrel had gone to the very back of the trap. This permitted the capture of very large squirrels which had been observed to back out of unmodified traps. Animals were individually marked by toe clipping. At each capture, identification number, time, location, detailed reproductive data (condition of vagina, lactation, position of testes) and weight were recorded. In 1973 and 1974, vaginal smears were prepared from females during the early part of the breeding season (May through June). The vagina was flushed with saline (0.8% NaCl) and a sample of the fluid was placed on a microscope slide, air-dried, stained with methylene blue, and examined for the presence of sperm. In 1973, laparotomies were performed on two females in May to observe the state of development of embryos. The females were anesthetized with Nembutol. A 1.5 cm incision was made in the lower right quadrant of the abdomen and embryos were counted and measured.

Usually traps were opened at 08:00, checked at 13:00 and checked and closed at 18:00. From 1969 to 1972 trapping occurred weekly from June through August. In 1973 and 1974, weekly trapping occurred from late March until August and then biweekly until October. Certain individuals were radio-tracked in 1972 and 1973 to monitor activity at critical points in the season. A detailed description of the radio-telemetry methods appears in Krohne et al. 1973).

RESULTS

In 1973, the first two females were captured on 16 May while the first male appeared on 22 May. In 1974 these events were delayed: 30 May and 31 May for females and males, respectively. Although trapping did not begin early enough in other years to document adult emergence, another aspect of the life history, the emergence of juveniles from the natal burrow, can be used to assess the possibility that 1973 and 1974 were unusual. Note in Table 1 that the dates of first appearance of juveniles in other years was very similar to those of 1973 and 1974. Indeed, 1973 had the earliest recorded emergence of juvenile females.

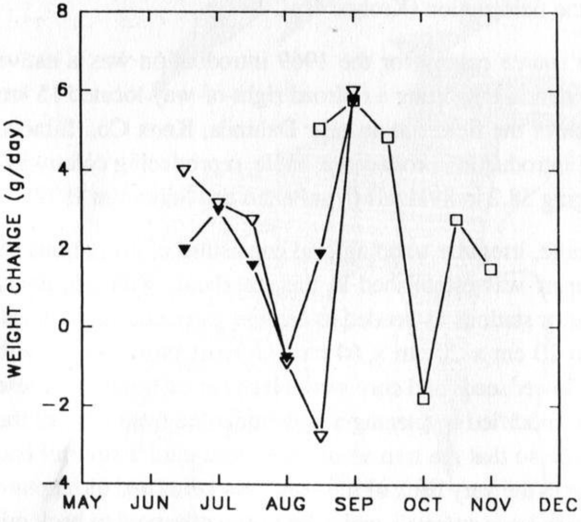

Figure 1. Seasonal weight changes. Mean weight change of adult males (closed triangles), adult females (open triangles) and juveniles (open squares) calculated for 14-day intervals.

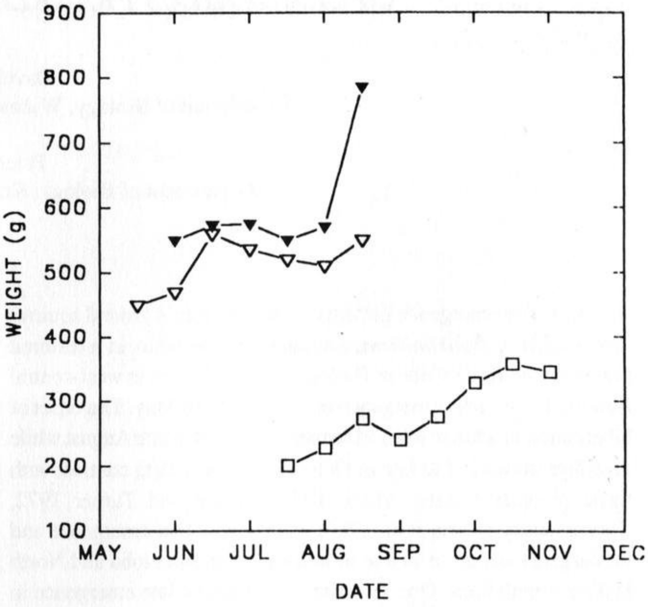

Figure 2. Mean weights. Mean weights of adult males (closed triangles), females (open triangles) and juveniles (open squares) over the course of the season.

All males and females captured in early spring were in peak breeding condition. The testes were completely descended and the scrotum was heavily pigmented. In females the vulva was open and swollen. Within two weeks after males appeared, vaginal sperm was detected in females, indicating that mating takes place soon or immediately after emergence from hibernation. Laparotomies performed on two females on 25 and 30 May, 1973 revealed 4 mm and 12 mm embryos respectively. Lactation began during the second and third week of June in all years. Males no longer had scrotal testes by mid-July and regression of the testes was complete by the first week of August.

Trapping records and radio telemetry showed that most adult males disappeared in early August, adult females in late August and most juveniles in September. Four juveniles carrying radios were active above ground in October. Three immerged during the second week of October; one was active until 25 October in 1973.

The patterns of weight change are shown in Figure 1. Female weight gain decreased as parturition approached. In mid June there was a precipitous weight loss associated with parturition that continued into the period of lactation. Adult males lost weight during mid-June. This corresponded to the end of the period of possible mating. Radio-telemetry and live trapping indicated that males undertook long-distance movements during this time. Juveniles had positive weight

Table 1. First emergence of juvenile Franklin's Ground Squirrels from the natal burrow.

	juvenile	
year	males	females
1970	18 July	19 July
1971	19 July	19 July
1972	27 July	21 July
1973	23 July	16 July
1974	21 July	21 July

changes immediately after emergence followed by a short period of weight loss and finally rapid weight gain just prior to immergence. The period of loss may be associated with a period of juvenile dispersal.

Adult males were consistently heavier than females and adult females were heavier than juveniles (Figure 2). Adult males entered hibernation at weights of 700-800g; females at approximately 600g and juveniles at 300-400g.

DISCUSSION

These data indicate that Franklin's ground squirrels in Illinois emerge in mid-to-late May. This contrasts with more northern populations that emerge up to one month earlier. For example, Murie (1973) reported emergence in mid-April in Alberta near the northern range limit. In Manitoba, emergence of males occurred in mid-April while females appeared the first week of May (Sowls, 1948; Iverson and Turner, 1972). In North Dakota males emerged in mid-April while females were first captured on 30 April (Choromanksy-Norris et al. 1986). Thus, emergence of our southern population was delayed relative to those at higher latitude. Recent data from Benjamin (1991) for a population in northwest Indiana at approximately the same latitude as our Illinois populations support the late emergence we report. In Benjamin's study the mean dates of emergence were 29 April and 3 May for males and females, respectively. Although his emergence dates are earlier than ours, they confirm that southern populations of Franklin's ground squirrels emerge later than northern populations.

As documented in the introduction, most ground squirrels emerge later at high latitude or altitude. Obviously, selection favors squirrels with an emergence pattern that avoids late winter storms but allows sufficient time above ground for the weight gains necessary to survive hibernation. At high latitude or altitude, the favorable season is so short that emergence may have to occur when inclement weather is still possible. Indeed, the arctic ground squirrel (*Spermophilus parryi*) at latitude 60°N emerge in April (Hock 1955), up to one month before Franklin's ground squirrels emerge at latitude 40°N in Illinois.

What selective factors might favor the late emergence of Franklin's ground squirrels in Illinois? We suggest two possibilities. First, May emergence avoids late winter storms. Michener (1977) emphasized the importance of this for a population of Richardson's ground squirrels. The patterns of weight loss in adult males and females (Figure 1) suggest that reproduction is an intensely energy demanding process. Late emergence prevents the potential problems of reproductive energy stress compounded by thermal stress or interruption of the food supply.

A second advantage relates to the preference of this species for dense cover and tallgrass prairie habitats. This species is extremely secretive and rarely ventures beyond the protection of dense cover (Krohne et al. 1973). Although the warm season grasses characteristic of Illinois prairies have begun growth in March, cover is not dense until at least the beginning of May, particularly if a burn has occurred. The northern prairies where the species emerges earlier are composed of cool-season grasses such as needlegrass (*Stipa spartea*), Junegrass (*Koeleria cristata*), Canadian wild rye (*Elymus canadensis*) and western wheatgrass (*Agropyron smithii*). In North Dakota, for example, the growth of these species begins as early as March and maximum height is attained by June (Whitman and Wali 1975, Weaver 1954). Indeed, 80% of the seasonal production of cool season grasses occurs before the end of June (Whitman 1954).

A major factor influencing the hibernation cycle in ground squirrels is the timing of reproduction such that juveniles have sufficient time to deposit adequate fat before the onset of hibernation. Any explanation of the late emergence of Franklin's ground squirrels in Illinois must allow for the over-riding importance of pre-hibernation weight gain by the juveniles. Our southern populations gained weight at rates similar to those reported by Choromansky-Norris et al. (1986) and hibernated at weights similar to those of northern populations (Iverson and Turner 1972, Choromanksy-Norris et al. 1986). Thus, both of the possible selective advantages of late emergence described above depend upon the lengthy growing season in Illinois that permits extended fall activity.

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SMALL MAMMALS OF THE OJIBWAY PRAIRIE PROVINCIAL NATURE RESERVE, WINDSOR, ONTARIO

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Abstract. The Ojibway Prairie Provincial Nature Reserve supports a unique and diverse small mammal assemblage. Studies in 1973 documented the role of habitat structure in affecting the distribution of two common rodent species (white-footed mouse, *Peromyscus leucopus* and meadow vole, *Microtus pennsylvanicus*). Periodic surveys through 1992 have revealed the presence of jumping mice (*Zapus hudsonius*), shorttail shrews (*Blarina brevicauda*), shorttail weasels (*Mustela erminea*) and chipmunks (*Tamias striatus*). Species diversity of the prairie small mammals exceeds that of any surrounding habitats that we have surveyed including those at Point Pelee National Park. The physiognomic diversity of habitats provided by the tallgrass prairie and oak savanna contributes to the variety of small mammal species.

INTRODUCTION

Small mammals are increasingly recognized as important indicator species in assessing natural and human disturbances of habitats (Szaro et al. 1988), and small mammals have been prominent in studies of population and community ecology. Ecologists have investigated competition for resources in small mammals (Grant 1972, Price 1978, Brown and Munger 1985), partitioning of space and food among species (Rosenzweig and Winakur 1969, M'Closkey and Fieldwick 1975, M'Closkey 1978, Dueser and Shugart 1979), and the impact of predators on small mammal distribution and behaviour (Kotler 1984, Brown et al. 1988). In small mammal ecology, habitat type is often thought to be important in providing refuges from predation and competition (Brown 1988). Many small mammal species that occur in the same geographic region may not occupy the same habitat because of possible competitive interactions (Brown and Nicoletto 1991).

In six different years since 1973, R.T. M'Closkey and graduate and undergraduate students at the University of Windsor have monitored the status of the small mammal fauna of the Ojibway Prairie Provincial Nature Reserve, Windsor, Ontario. The Ojibway Prairie first attracted our attention because of the high diversity of small mammal species. In addition, the tallgrass prairie at Windsor is part of the prairie peninsula (Transeau 1935, Rogers 1966) within the prevalent Eastern Deciduous Forest Biome. Therefore, the diversity and composition of the small mammal fauna may reflect the idiosyncratic features of isolated prairie habitat. The purpose of this paper is to summarize our data on the relative abundance and diversity of small mammal species at the Ojibway Prairie. We report previously unpublished census records of mammals.

METHODS

Study Site and Mammals

The Ojibway Prairie tallgrass community is unique to this part of North America (Rogers 1966), and contains a small mammal fauna which is typically associated with seral stages of Eastern Deciduous Forest.

Rogers (1966) described the 81 ha reserve as an oak savanna dominated by *Quercus palustris* with woody vegetation composed of *Cornus racemosa*, *Rhus* spp, and *Populus* spp. Grasses include *Calamagrostis canadensis*, *Spartina pectinata*, *Andropogon gerardi*, *Panicum virgatum*, and *Sorghastrum nutans*. Common herbaceous plants were *Solidago canadensis*, *Baptisia tinctoria*, *Viola sagittata*, *Aster* spp. and *Fragaria virginiana*. The open understory of the oak savanna was frequently dominated by ferns (*Pteridium aquilinum*). During the years of the mammal census precipitation averaged 970 mm with a range of 802 to 1108 mm. The thirty-year (1961-1990) mean precipitation for Windsor (Environment Canada 1993) is 902 mm.

Three orders of terrestrial small mammals occur at the Ojibway Prairie. Rodents (Rodentia) dominate the small mammal fauna. The most common species are *Peromyscus leucopus* (white-footed mouse) and *Microtus pennsylvanicus* (meadow vole). Normally, these species segregate by habitat type, but in ecotone and secondary succession habitat they may occur together (M'Closkey 1975). Two other rodent species (*Zapus hudsonius*, meadow jumping mouse; *Tamias striatus*, eastern chipmunk) are present, although usually in low numbers. *Mustela erminea* (shorttail weasel, Carnivora) is present in small numbers. *Blarina brevicauda* (shorttail shrew, Insectivora) is present and is a major predator on arthropods and other invertebrates.

Mammal Census

We have conducted periodic live-trapping from 1973 through 1992. Some of this work has been previously published (M'Closkey and Fieldwick 1975), and other census work has appeared in a Master's degree thesis (Wilson 1983)

Table 1.Captures of small mammals (N/100 traps set) at Ojibway Prairie.

YEAR	White-footed Mouse	Vole	Jumping Mouse	Chipmunk	Shrew	Weasel
1973	11.1	9.1	0.2	0	1.1	0.5
1984	17.4	3.1	0	0.7	0.7	0.4
1985[1]	19.0	5.3	0	0	1.2	0
1986	9.4	3.3	0.4	0	0.2	1.1
1991	4.9	3.7	1.4	0.4	2.3	0.2
1992	25.6	0.5	0	0	1.0	0.2

[1] Source: Ceman 1986.

and two undergraduate honours theses (Ceman 1986, Gajda 1989). In addition, students in Field Biology at the University of Windsor provided census data for 1984, 1986, 1991 and 1992. In 1981 and 1988, records of captures were kept only for white-footed mice and voles. In addition to these surveys, Morris (1979) published detailed records of his small mammal census at the Prairie.

Mammals were trapped in Sherman aluminum live traps baited with wild bird seed and supplied with cotton during cool weather. Traps were not baited specifically for weasels and shrews and our efforts may have underestimated their numbers. Trapping was conducted during the late summer and early fall. In addition, in 1973, trapping was also conducted in mid-summer. Captured individuals were identified, sex and age-class determined, and released. In 1973 and 1981 voles and white-footed mice were toe clipped for individual identification. From 1984 through 1992 the mammals were released without marking. Therefore, we do not estimate small mammal density (number of different individuals per unit area) because it was not possible to distinguish individuals. We estimate density as the number of captures of mammals per 100 traps set. No doubt some individuals were captured more than others.

The trapping effort varied from year to year although the same trap lines were used each year. The total number of traps set varied from 410 in 1992 to 1040 in 1973, and the mean number of traps set per year was 640. Because of this variation in trapping intensity, there is the possibility that estimates of diversity and capture frequency would be biased by differential effort. To examine this potential bias we performed correlations between estimates of species diversity, total mammal captures per 100 traps set, and captures of *P. leucopus* per 100 traps set. Correlation coefficients ranged from - 0.12 to 0.26 (all $P > 0.6$). Therefore, our estimates of diversity and abundance were independent of our field effort. For example, our highest estimate of species diversity (in 1991) was obtained with only 512 traps set.

Where census data are reported for all species (1973, 1984, 1985, 1986, 1991, 1992) we represent mammal species diversity by both the number of species present and by an index of diversity that incorporates both the number of species and their relative abundance. This index is the inverse of Simpson's formula $(1/\Sigma p_i 2)$, where p_i is the proportional abundance of the i^{th} species. This index has the attractive feature that if all species are equally abundant then $1/\Sigma p_i 2 = S$, where S is the number of species in the census. Where only one species is present the index is 1.0, its minimum value.

RESULTS

Small Mammal Captures

There are sufficient census data for six different years to report the captures of six small mammal species (Table 1). For two additional years (Wilson's survey, 1981; Gajda's survey, 1988) captures were reported only for white-footed mice and meadow voles. These mammals dominate the community, comprising from 66 to 94% of all captures, depending on year. Jumping mice, shrews, weasels, and chipmunks are either absent or capture rates are low.

The complete census for the two dominant species is shown in Figure 1. Our 1991 census revealed the fewest captures of mice that we have observed and in 1992 white-footed mouse captures were the highest of any year. The combined capture rate of mice and voles was 10 captures per 100 traps set in 1991. In 1973, M'Closkey and Fieldwick (1975) recorded a combined capture rate in excess of 20 mice and voles per 100 traps set, with roughly equal numbers of both species.

Habitat Use

Although small mammals overlap in their local distribution and may be captured at the same trap stations, there are differences among the species in microhabitat preference

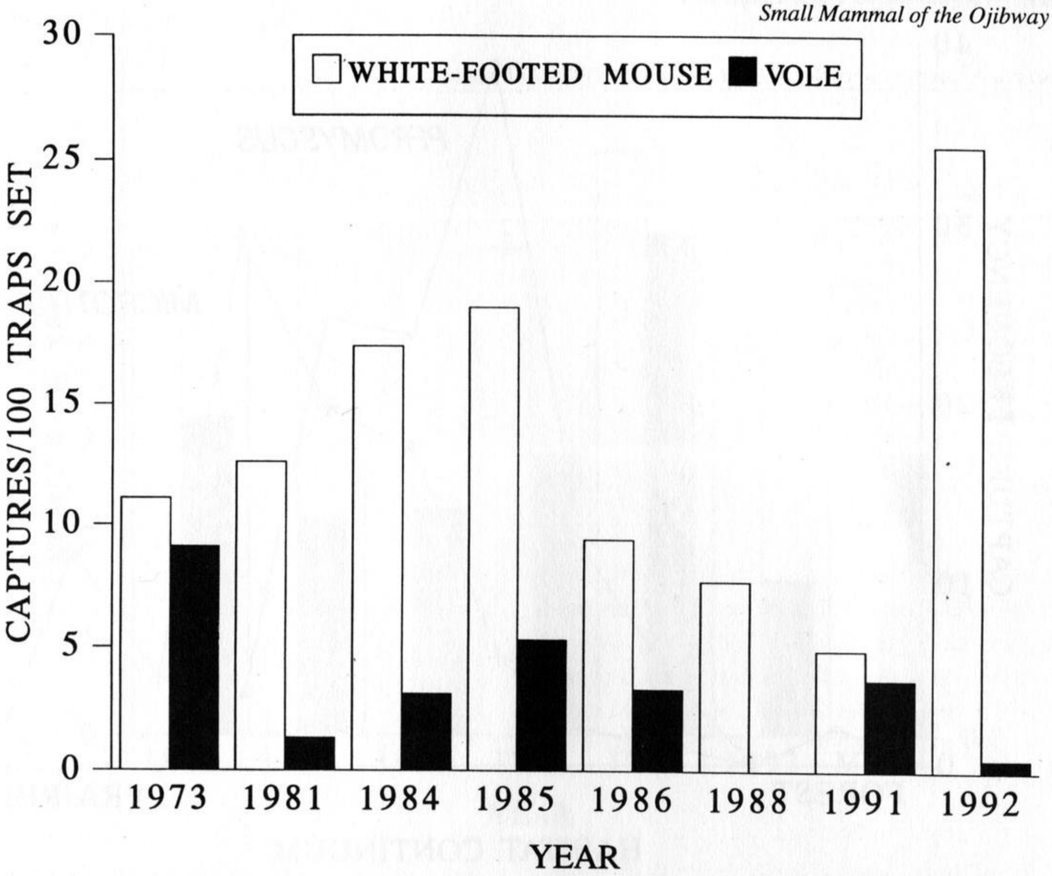

Figure 1. Captures (N/100 traps set) of white-footed mice (open bars) and meadow voles (closed bars) at the Ojibway Prairie. Sources: 1981, Wilson 1983; 1985, Ceman 1986; 1988, Gajda 1989.

(Figure 2). The habitat continuum is described by a linear combination of several habitat variables including tree density, foliage diversity, and depth of the mat of perennial grasses (M'Closkey and Fieldwick 1975). Trees and high foliage diversity (forest end of the continuum) favour white-footed mice, whereas open habitat with a thick mat of perennial grass (from which voles construct surface runways) favours voles. In addition, jumping mice and shrews occur at the prairie end of the continuum, chipmunks in the forest, and weasels are found in all habitat types. Morris (1979) reports some differences from the pattern we report here. For example, he encountered jumping mice in mature forests in Southwestern Ontario.

Small Mammal Species Diversity

Mammal diversity at the Ojibway Prairie is depicted in Figure 3 for those years in which the captures of all small mammal species were reported. We consistently trapped five species. The quantitative estimates of species diversity (the inverse of Simpson's index) incorporates both the number of species captured as well as their relative abundance. This estimate of diversity shows more variation among years than does the number of species present. This variation simply reflects the change in numerical dominance among the mammals from year to year. For example, white-footed mice comprised 38% (1991) to 78% (1984) of all mammal captures. The more equitable number of captures of different species in 1991 (Table 1) is responsible for the high estimate of species diversity (3.7).

DISCUSSION

Periodic surveys of small mammals at the Ojibway Prairie since 1973 have revealed consistently high species diversity. Many authors have demonstrated the relationship between small mammal species diversity and structural characteristics of habitats (Rosenzweig and Winakur 1969, M'Closkey 1978, Price 1978, Morris 1979, Brown 1988). In addition, small mammal distribution is associated with seral stages of ecological succession (Connor 1953, Hirth 1959, Pearson 1959, Wirtz and Pearson 1960, Getz 1961 a,b, Shure 1970, M'Closkey 1975, Fox 1982, Price and Waser 1984). The uniqueness of the small mammal species composition of the prairie is emphasized by three points. First, the prairie mammals are derived from species typical of wet meadows and grassland (vole, jumping mouse) as well as those characteristic of forest and shrub habitat (white-footed mouse, chipmunk). Second, the forest surrounding the Ojibway Prairie has no jumping mice or voles (M'Closkey and Hecnar, unpublished), a point which illustrates the island-like mam-

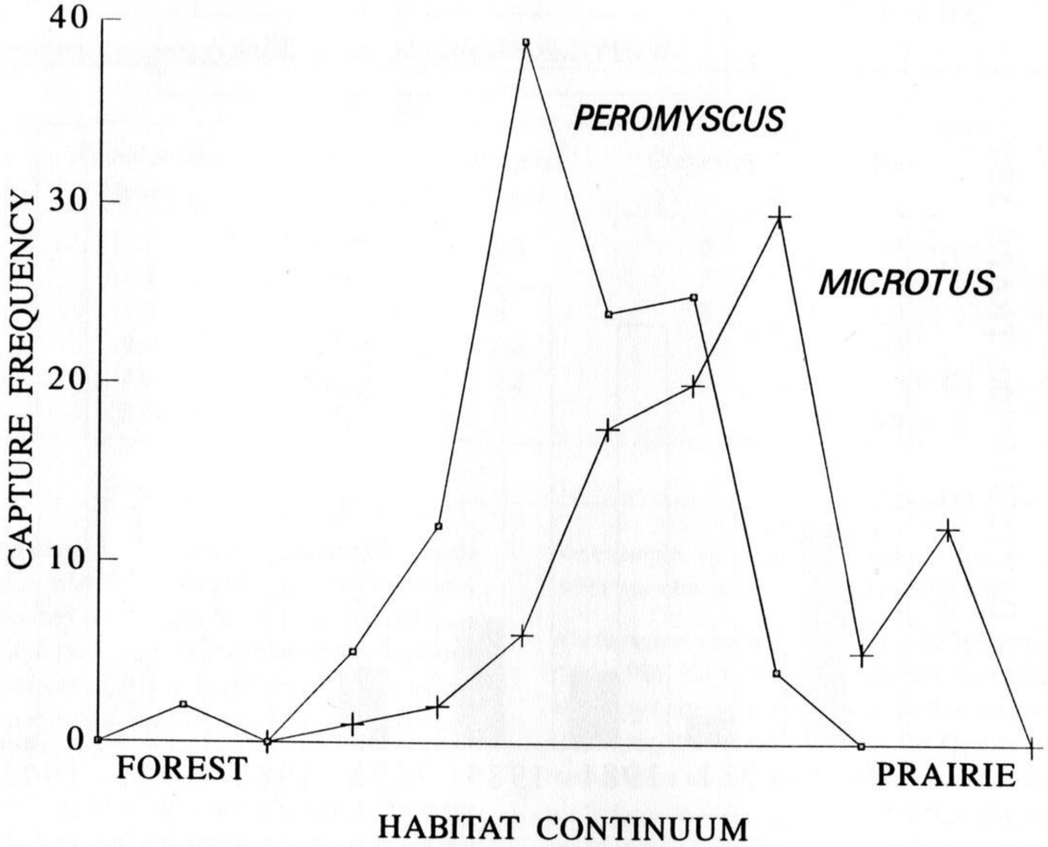

Figure 2. Total captures of white-footed mice (*Peromyscus*) and voles (*Microtus*) on a gradient of habitat structure at the Ojibway Prairie (from M'Closkey and Fieldwick 1975).

mal fauna of the prairie relict. Finally, both voles and white-footed mice can be trapped at the same trap station. This is unusual because Baker (1968) noted the complementary distribution of these species in wooded (mouse) and grassland (vole) habitat elsewhere in North America.

Ecologists have become increasingly aware of the roles of disturbance and ecological succession in determining patterns of species diversity (Connell 1975, 1978; Connell and Slatyer 1977, Sousa 1984). Fire, as a source of disturbance, has been the subject of investigations on plant (Daubenmire 1968, Collins 1987, Riggan et al. 1988) and animal (Lawrence 1966, Fox 1982, Price and Waser 1984, Geluso et al. 1986, Wirtz et al. 1988, Clark and Kaufman 1990) distribution and diversity. These studies clearly suggest that small mammals show species-specific responses to fire and successional changes during postfire succession. The specific mechanisms producing the responses of the mammals is not typically identified (Price and Waser 1984), although modified vegetation structure is strongly implicated. Fox (1982) suggests there is a sequence of species replacement during postfire succession, and the pattern is contingent on the unique habitat requirements of the different species. The fire regime plays a pivotal role in promoting small mammal species diversity.

It is unlikely that fire, as a source of mortality, causes a loss of diversity. Geluso et al. (1986) and Lawrence (1966) report that fire-induced mortality in small mammals is infrequent. However, Wirtz et al. (1988) suggest that some small mammal species may be more prone to mortality during fires because of their specialized microhabitat requirements. It is also apparent that some small mammal species are fire specialists (Wirtz et al. 1988, Clark and Kaufman 1990) and quickly invade habitats during post-fire succession.

Although we have not examined species-specific responses of the Ojibway mammals to periodic burning, we can foresee changes in the small mammal fauna in the absence of fires. Curtis (1959) noted that unburned prairie habitat would eventually be replaced by surrounding forest. By inference, both voles and jumping mice should disappear from the Ojibway Prairie without periodic burning. In addition, M'Closkey (1975) predicted the loss of voles during ecological succession from mixed grassland-forest habitat at nearby Point Pelee National Park. Consequently, diversity may be reduced without the disturbance regime provided by fire.

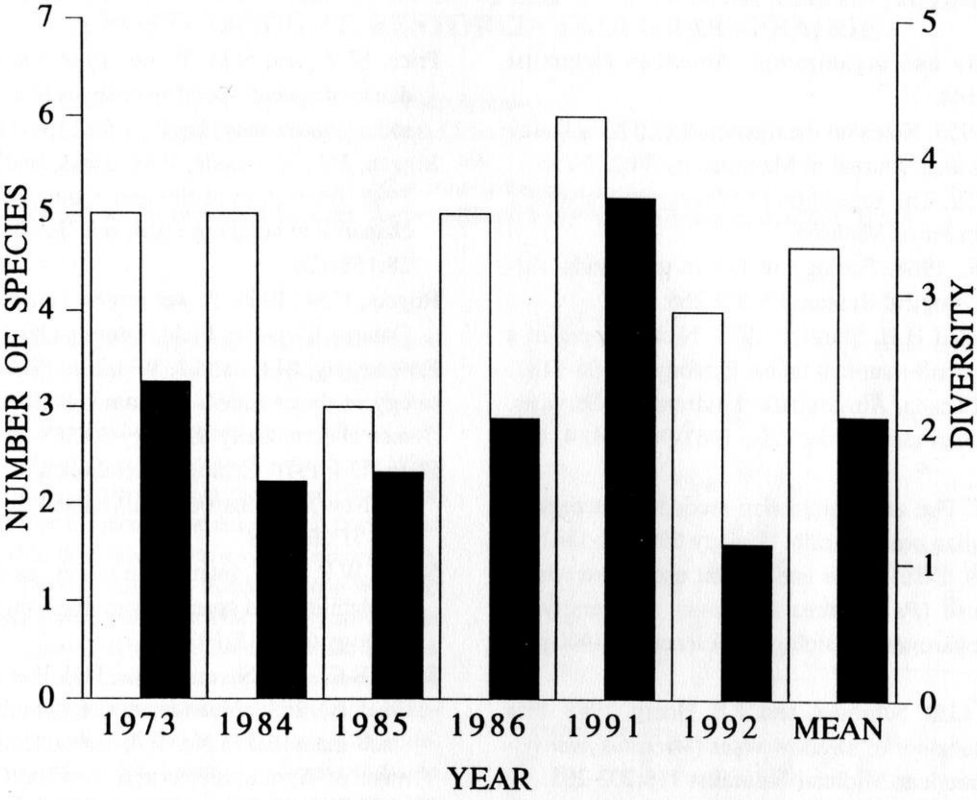

Figure 3. Number of species (open bars) and an index of species diversity (closed bars) of small mammals at the Ojibway Prairie.

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A DRAMATIC INCREASE OF THE MEADOW JUMPING MOUSE (*ZAPUS HUDSONIUS*) IN A POST-DROUGHT, RESTORED, TALLGRASS PRAIRIE

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Abstract. During a continuing live-trap study of small mammals in a restored, tallgrass prairie on the Knox College Biological Field Station, the summer trapping session of 1991 recorded a 25 fold population increase of the meadow jumping mouse (*Zapus hudsonius).* Results suggest that the early summer drought during 1991, following the 1990 recovery period from the severe drought of 1988-89, set the stage for the increase of this species. During this same period, the prairie deer mouse (*Peromyscus maniculatus*), dominant during the 1988-89 drought, decreased along with two vole species (*Microtus pennsylvanicus* and *M. ochrogaster*). This negative correlation suggests that interspecific competition between jumping mice and more commonly occurring rodent species may be the controlling factor determining the low numbers of the jumping mouse recorded in previous studies in this prairie. The white-footed mouse (*Peromyscus leucopus*) normally a forest and prairie edge species, deeply invaded the prairie grid to a greater degree than in previous studies.

INTRODUCTION

This report is part of an on-going study of the response of small mammal populations to the drought of 1988 and the post-drought response of these populations during the years following, on a restored tallgrass prairie in west-central Illinois (Schramm et al. 1992). This phase of the study continued to follow the presence and relative abundance of the different small mammal species occurring in the study area during 1991. Intensive summer live-trapping revealed a dramatic increase of the meadow jumping mouse (*Zapus hudsonius*). This increase appeared to be correlated with a decrease in numbers of other species previously present during the drought. The meadow jumping mouse is widely distributed over mesic grassland and meadow habitats but is rarely abundant. In all previous live-trapping studies conducted on this prairie, it was encountered only in very low numbers of 1 to 3 individuals per summer (Schramm 1970, Moreth and Schramm 1973, Schramm and Willcutts 1983, Schramm et al. 1992). The sudden and dramatic increase of up to 50 individuals of this species in a restored prairie that has been under observation for almost three decades, indicates there is still much to be learned about the small mammals in this habitat and their response to weather extremes and interspecific competition.

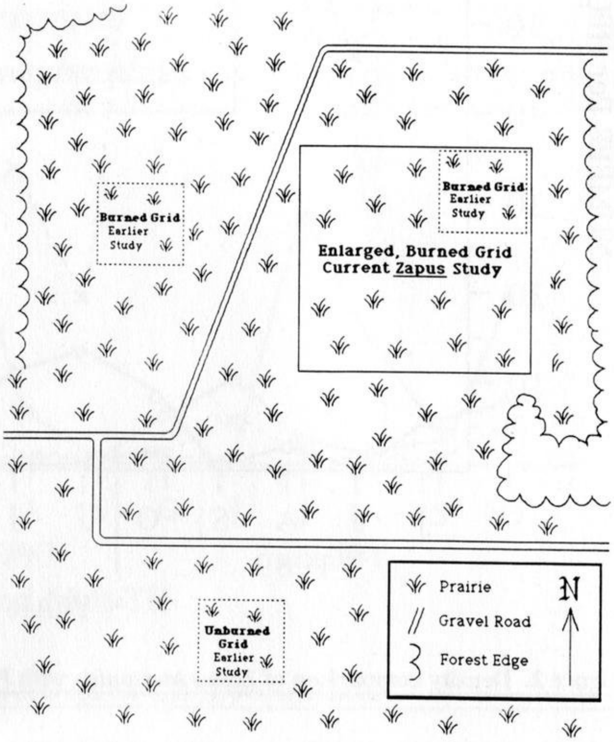


Figure 1. Map comparing location and habitat of the large trapping grid of this study with the smaller grids of the earlier study.

METHODS

Study Area

This study was conducted on the Knox College Biological Field Station located 7.2 km south of Victoria, Knox County, Illinois from May 20, 1991 through March 13, 1992. The study area (Figure 1) was a 20 ha restored tallgrass prairie consisting of prairie grasses and forbs previously described by Schramm et al. (1992). The initial live-trapping study of the drought and post-drought small mammal populations was conducted on three 0.16 ha plots (Figure 1, dotted lines) laid out as 25 station grids with 10 m intervals between stations (Schramm et al. 1992). Starting in August of 1991, because of the increasing numbers of jumping mice, the burned study plot (Figure 1, solid lines, burned March 1991) was increased in size to 1.96 ha with 64 live-trap stations at 20 meter grid

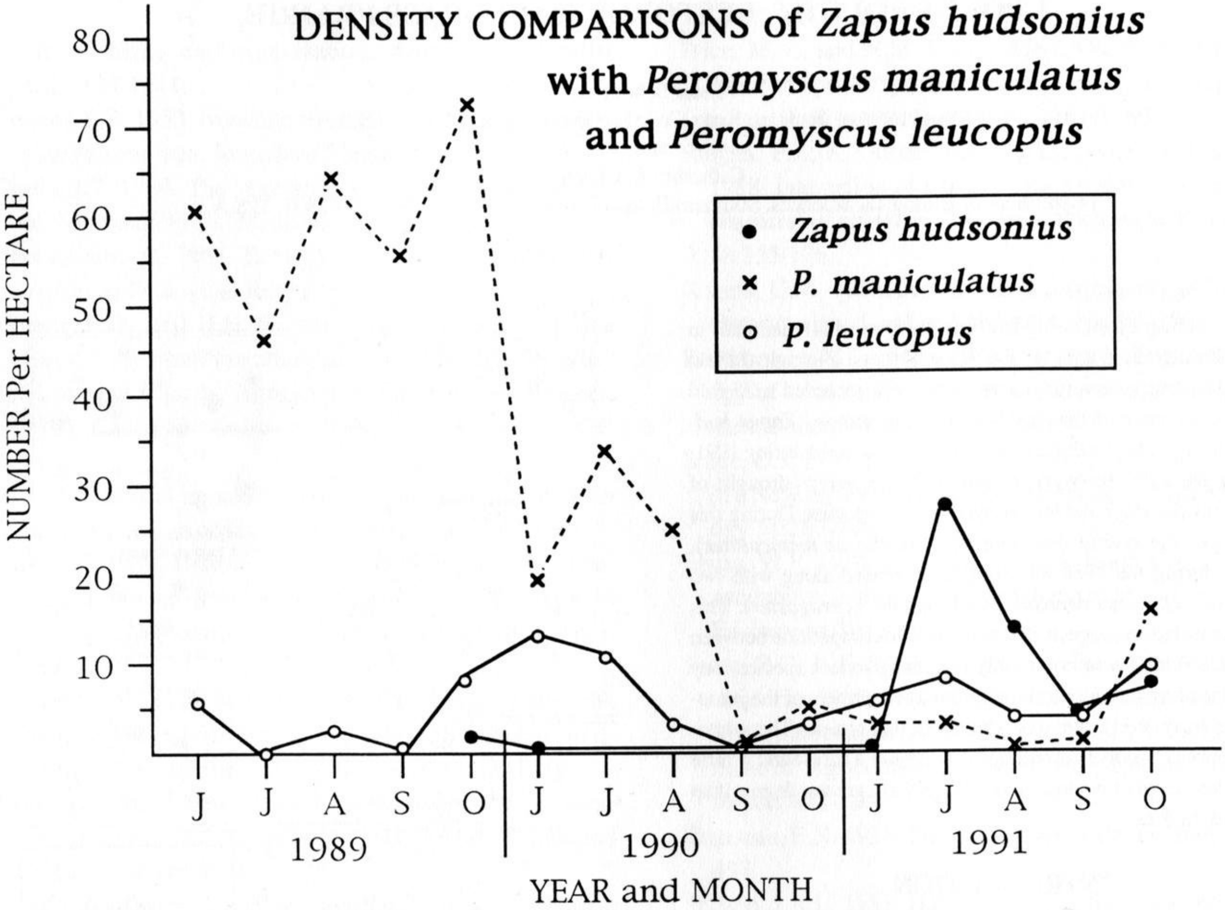


Figure 2. Density comparison of *Zapus hudsonius* with *Peromyscus maniculatus* and *P. leucopus*.

intervals, to accommodate the more wide-ranging movements of this species (subsequent florescent powder and radio-tracking experiments with this species during the summer of 1992 have substantiated that this species moves well beyond the limits of the smaller grid size). In previous studies on this prairie (Schramm 1970, Moreth and Schramm 1973, Schramm and Willcutts 1983, Schramm et al. 1992), the numbers of jumping mice encountered have been very small (2-3 individuals per summer), but it is very clear that jumping mice almost always avoid unburned areas. Thus, the enlarged trapping plot, located in an area burned annually (March) since 1987, became the main study area and the other two smaller plots were discontinued. Figures 2 and 3, presenting the density data discussed in this paper, include densities occurring in the earlier (Schramm et al. 1992) as well as the most recent phase of this study.

Trapping Procedure

Each trapping station was trapped with two Sherman live-traps per station. In this phase of the study, twenty trapping periods, were conducted from May 20, 1991 to March 13, 1992, consisting of 4 trapping nights with 7-10 day intervals between trapping periods. All traps were removed between each period. Standard capture-mark-recapture techniques were used with all animals uniquely marked with a numbered aluminum ear tag. For each capture the trapping period, date, grid, station number, species, tag number, sex, weight, estimated age, reproductive condition, and any distinguishing characteristics were recorded before release at the site of capture. During the summer months, a combination of commercial bird seed and sunflower seeds was used for bait. When temperatures dropped below 40° F a combination of bird seed, peanut butter and rolled oats was used and cotton nesting material was placed in each trap.

ANALYSIS OF DATA

During the trapping of the smaller grid, the density (individuals/ha) for each trapping period was estimated by dividing the number of animals captured by the area of the grid plus an additional boundary strip of 10 m. Thus, the effective area being sampled in the earlier phase of the study was a 60 m by 60 m square or 0.36 ha. For density estimates on the enlarged grid, the number of animals captured was divided by the area of the grid itself (140 m by 140 m or 1.96 ha) without adding a boundary strip. We believe the grid size

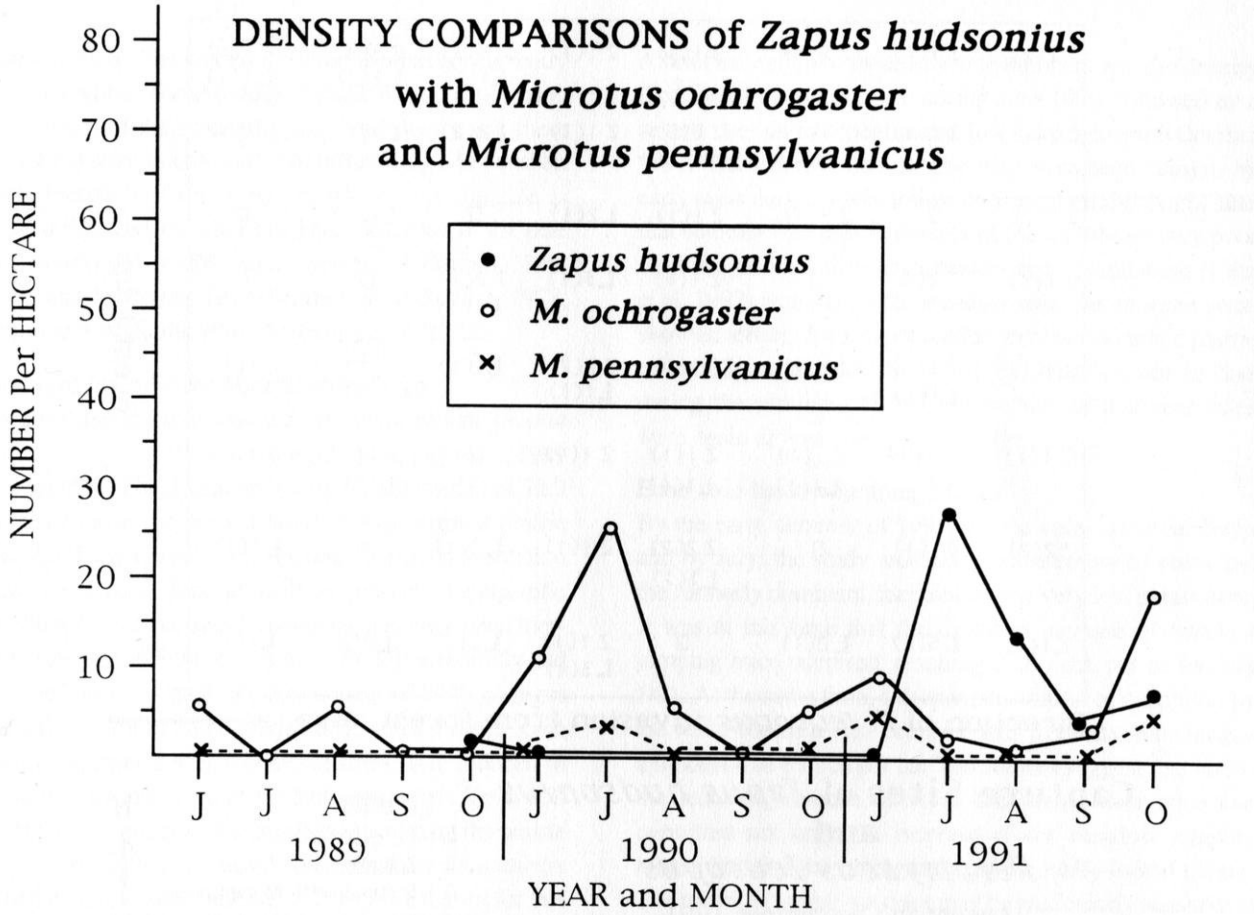


Figure 3. Density comparison of *Zapus hudsonius* with *Microtus ochrogaster* and *M. pennsylvanicus*.

change does not compromise our density estimates and was necessary to more accurately analyze the numbers and movements of jumping mice. We recognize the inherent problem of sampling different species with one procedure but we believe the frequency and regularity of trapping periods and intensity of trapping (2 traps per station) resulted in valid estimates and comparisons.

RESULTS

In addition to the meadow jumping mouse, other species encountered during 1991 included the white-footed mouse (*Peromyscus leucopus*), the prairie deer mouse (*Peromyscus maniculatus*), the prairie vole (*Microtus ochrogaster*), and the meadow vole (*Microtus pennsylvanicus*). There was a striking change in the species dominance observed during the 1991 summer as compared to the preceding years.

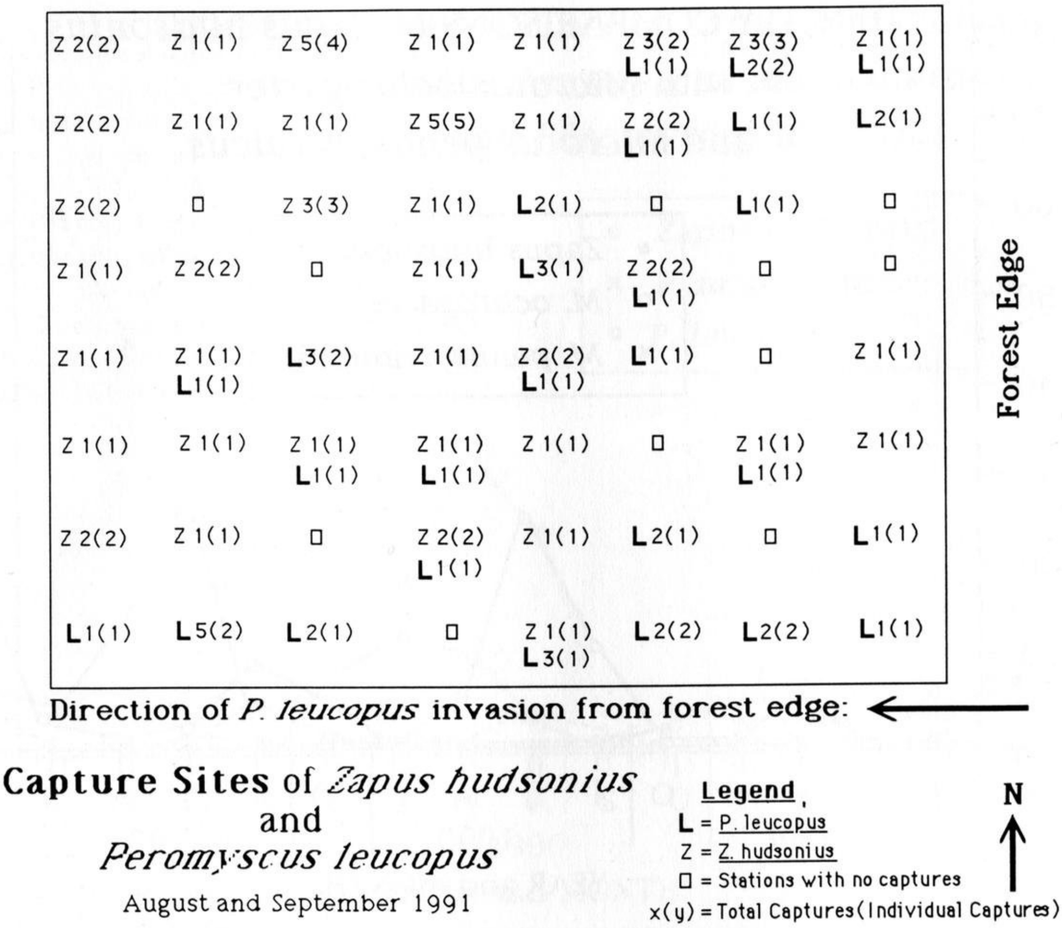
Dominance of the Meadow Jumping Mouse

Figures 2 and 3 compare the density of the meadow jumping mouse to the other species of rodents present. This species went from an almost non-existent status during 1989 and 1990 to 27.8 mice per ha by July 1991. Numbers dropped to 13.8 per ha in August, 4.6 per ha in September and recovered back up to 8.2 per ha in October, just before hibernation. Thus, this rare species continued to maintain a much higher than usual presence throughout most of the growing season of 1991.

Density of *Peromyscus* Species

Figure 2 compares jumping mouse density to densities of the prairie deer mouse and the white-footed mouse. The prairie deer mouse was the dominant species present during the drought (1988) and the year immediately following (1989), (Schramm et al. 1992), occurring in densities as high as 72.2 per ha in October of 1989. It was reduced to less than half that number during 1990 and by 1991 its dominance of the study area had come to an end.

In the earlier phases of this study (summers of 1989 and 1990) white-footed mouse captures occurred only along the eastern portion (eastern one-third) of the small, burned grid (Figure 1). This typically woodland and prairie edge species (Clark et al. 1987, Kantak 1983, Synder and Best 1988) normally invades only into the peripheral areas of these prairie plots and not deeply into the center (Schramm and



Z 2(2)	Z 1(1)	Z 5(4)	Z 1(1)	Z 1(1)	Z 3(2) L1(1)	Z 3(3) L2(2)	Z 1(1) L1(1)
Z 2(2)	Z 1(1)	Z 1(1)	Z 5(5)	Z 1(1)	Z 2(2) L1(1)	L1(1)	L2(1)
Z 2(2)	□	Z 3(3)	Z 1(1)	L2(1)	□	L1(1)	□
Z 1(1)	Z 2(2)	□	Z 1(1)	L3(1)	Z 2(2) L1(1)	□	□
Z 1(1)	Z 1(1) L1(1)	L3(2)	Z 1(1)	Z 2(2) L1(1)	L1(1)	□	Z 1(1)
Z 1(1)	Z 1(1)	Z 1(1) L1(1)	Z 1(1) L1(1)	Z 1(1)	□	Z 1(1) L1(1)	Z 1(1)
Z 2(2)	Z 1(1)	□	Z 2(2) L1(1)	Z 1(1)	L2(1)	□	L1(1)
L1(1)	L5(2)	L2(1)	□	Z 1(1) L3(1)	L2(2)	L2(2)	L1(1)

Capture Sites of *Zapus hudsonius*
and
Peromyscus leucopus
August and September 1991

Legend,
L = P. leucopus
Z = Z. hudsonius
□ = Stations with no captures
x(y) = Total Captures(Individual Captures)

Figure 4. Capture sites and invasion pattern of *Peromyscus leucopus* from the forest edge into the large grid, August and September 1991.

Willcutts 1983, Schramm et al. 1992). Densities of this species in the eastern edge of the prairie went from densities of 6.0 per ha in June and 0.0 per ha in July of 1989 to 13.9 per ha in June and 11.1 per ha in July of 1990, and held its own in 1991 reaching a density of 8.3 per ha by July of that year. We believe these early to mid-summer changes are due to the decline of prairie deer mouse numbers during this same time. In addition, during 1991, in the absence of high deer mice numbers, this species exhibited a much deeper penetration out into the prairie than in previous years, sharing to a degree, much of the enlarged, burned grid with the meadow jumping mouse. Figure 4 illustrates the capture positions of this species deep into the large grid.

Density of Vole Species

Figure 3 compares meadow jumping mouse densities to densities of the prairie vole and the meadow vole on the burned grid. Vole populations were extremely low during the drought and post-drought years (Schramm et al. 1992). The post-drought years of 1989, 1990 and even 1991 had rainfall reduced well below normal on the field station and immediate vicinity. Vole populations attempted recoveries but re-occurring dry periods probably continued to keep their numbers low. The meadow vole was almost non-existent throughout the entire study, from 1988 to 1991, in both the burned and unburned areas. Only during the spring and fall of 1991 did it reach densities of slightly over 5 per ha presumably in response to increased moisture at these times.

The prairie vole occurred in somewhat higher numbers than the meadow vole during the post-drought years, particularly in 1990, reaching 26 per ha in July but dropped to very low numbers of 2 per ha in July of 1991 coinciding with the surge of meadow jumping mouse numbers. It was not until the return of more normal rainfall in late summer and fall of 1991, that the prairie vole had a significant increase in density to 18.4 per ha in October.

DISCUSSION

The most obvious question that arises from the results of this study is what was responsible for the dramatic increase of the meadow jumping mouse, a normally rare species in this grassland habitat. The second question is what concurrently allowed the white-footed mouse to make a deep penetration into the center of the prairie habitat. And finally, are these two observed phenomena related or influencing one-another. Our interpretation of the causal factors in this situation is strongly influenced by what has been observed in the past studies conducted in this same prairie (Schramm 1970, Springer and Schramm 1972, Moreth and Schramm 1973, Schramm and Willcutts 1983, Schramm et al. 1992).

Reduction of Prairie Deer Mice Sets the Stage

The prairie deer mouse was the dominant rodent present during the drought of 1988, and the post-drought year of 1989 (Schramm et al. 1992), reaching very high densities of 72.2 animals per ha in the burned areas of this restored prairie (Figure 2). The reasons for this increase included adaptation to more xeric conditions as well as reduced interspecific competition from other small mammals, and have been thoroughly discussed in Schramm et al. (1992). It essentially had this prairie almost to itself. By the summer of 1990, changes were in effect. Rainfall increased, prairie voles showed some recovery, and prairie deer mouse densities were reduced to less than half the densities of the summer before. Yet it still held forth that summer as the dominant species on the prairie until a severe decline occurred in September. Its numbers remained very low until October of 1991. The reason for this decline is not entirely clear but the authors believe the drought-caused population high of this species had finally run its course. Prairie deer mouse numbers in this restored prairie have never been consistent or followed a definite pattern. In some of the earlier studies it was seldom captured or occurred only in modest numbers (Schramm 1970, Springer and Schramm 1972, Moreth and Schramm 1973). In later studies it became a more important member of the community (Schramm and Willcutts 1983).

Continuing Low Numbers of Voles During the Post-Drought Years

With one exception, outlined below, the voles remained very low during this entire period. The drought greatly reduced both species of voles in all the prairie habitats on the field station (Schramm et al. 1992) and the sporadic dry periods during the post-drought years continued to keep them very low, particularly the meadow vole. This species was almost non-existent during the drought and did not fare much better during the post-drought years. A number of studies have indicated that it prefers mesic meadows and prairies with some litter present (Getz 1961, Miller 1969, Schramm 1970, Moreth and Schramm 1973, Schramm and Willcutts 1983, Synder and Best 1988, Vacanti and Geluso 1985). The absence of litter in this burned area probably also contributed to its low numbers.

A brief exception to these low vole numbers was the density increase of the prairie vole during June 1990, followed by a severe decline and continuing low numbers until October 1991. The increase and decline may have been caused by early rains during 1990, follow by a local mini-drought later that summer (the prairie grasses of these plots set very poor seed that year). This species prefers dry, upland areas (Getz et al. 1987) and, unlike the meadow vole, can in some years show an affinity for and population increase in burned prairie as well (Schramm and Willcutts 1983). This was not the case during the summer of 1991 and by July of that year voles were again almost non-existent in the prairie.

Enter the Meadow Jumping Mouse

By the early summer of 1991, prairie voles were declining and by July, the study area was almost empty of voles and the formerly dominant deer mouse was very low in numbers. It was at this time that the dramatic increase of meadow jumping mice occurred, reaching 27.8 mice per ha by July 1991. At the same time, a deeper penetration of the prairie by the white-footed mouse occurred with a density remaining at a modest 4 to 8 mice per ha. The authors suggest that it was the reduced presence of voles and prairie deer mice that permitted not only the increase of the meadow jumping mouse but also the immigration of the white-footed mouse. The meadow jumping mouse may be particularly sensitive to interspecific competition and presence of other grassland rodents.

In an important study by Boonstra and Hoyle (1986) in southern Ontario, it was determined that meadow jumping mouse populations compete with and are perennially low because of the presence of meadow vole populations. On experimental grids with all the voles removed, jumping mice densities reached 28.6 to 37.1 per ha in two years time, on grids where all female or all male voles were removed, jumping mice densities reached 11.4 to 20.0 per ha, and on control grids with normal meadow vole numbers present, the jumping mice densities remained at a modest 1.4 to 5.7 per ha. The 28.6 per ha value observed in the vole removal grid is very similar to the high of 27.8 per ha observed in this study. The Boonstra and Hoyle study strongly suggests that the meadow jumping mouse is very sensitively tuned to the presence or absence of meadow voles, and our present study further suggests that it is equally sensitive to the presence or absence of the prairie deer mouse.

White-footed Mouse Response and Prairie Invasion

During the summer of 1990 the white-footed mouse increased to 13.9 per ha by June and then declined to very low numbers again by early fall, coinciding with the mid-summer increase of prairie deer mice (Figure 2). It was still caught mainly on the east one-third of the original smaller grid in close proximity to the forest edge (Figure 1). This edge dispersion pattern changed dramatically in 1991. Figure 4 illustrates the deep penetration of the white-footed mouse into the large grid. We believe the primary reason for this invasion was the greatly reduced presence of the prairie deer mouse and the increase of available space.

Nichols and Conley (1981) found some evidence of competitive exclusion of white-footed mice by meadow jumping mice with the former species establishing consecutive capture patterns only after the latter species began to decline. In the present study, such exclusion was not observed and may be explained on the basis of the sudden availability of a large amount of space that both species could share. Futhermore, it may well be that niche overlap of the grassland dwelling meadow jumping mouse with the forest dwelling white-footed mouse is less than niche overlap with grassland species such as the prairie vole and the prairie deer mouse.

CONCLUSIONS

In summary, this study documents an unusually high number of meadow jumping mice occurring in a regularly burned, restored prairie, following post-drought adjustments and reductions in the numbers of other rodent species sharing the same habitat. The data suggest that reduction in numbers of the prairie deer mouse and the continued low numbers of voles may be contributing factors to the meadow jumping mice increase. This same reduction may also have encouraged the influx of white-footed mice more deeply into the prairie than usual.

ACKNOWLEDGMENTS

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DIVERSITY, ABUNDANCE, AND DISTRIBUTION OF BUTTERFLY SPECIES IN REMNANT AND TALLGRASS PRAIRIE

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Abstract. A comparative study of butterflies was conducted in restored and remnant prairies in Knox, Mercer, Warren, and Henry Counties in west-central Illinois comparing species diversity, abundance, and habitat distribution in prairies that had been both burned and unburned the previous springs. The time table for these studies encompassed two complete nonconsecutive growing seasons from May 6, 1988 to October 15, 1988 and May 11, 1990 to September 26, 1990. Location, sublocation, date, time, temperature, and wind were noted to compare rates of activity change with different weather factors and sites. Visual census of butterfly numbers in all areas was used to show species diversity, inter and intra butterfly species associations, and plant associations. Seasonal phenology and plant associations were compared and contrasted between observed and expected results. Endemic skippers were searched for but not found.

INTRODUCTION

Butterflies can be found in a wide variety of habitats. Some butterflies, such as the monarch (*Danaus plexippus* Linnaeus), are associated with more than one type of habitat. Other butterflies such as the arogos skipper (*Atrytone arogos* Boisduval and LeConte) can be found only in association with prairie habitat. These endemic butterflies can serve as ecological indicators, suggesting the health of the areas they frequent (Tdkaesky 1988).

In west-central Illinois, tallgrass prairie interspersed with forest once made up most of the area. However, less than one percent of the original prairie is now left. This remnant prairie primarily exists along railroad tracks, in nature preserves, and in a very few cases, private land. In most cases the nature preserves are old cemeteries the size of a hectare or less. Most roadways have been either sprayed or mowed limiting the diversity and numbers of prairie forbs and grasses in these areas. Because of the lack of true prairies, restoration is now taking place. With restoration however, comes the question concerning the similarities and differences between the remnant and restored prairies and the invertebrates that inhabit them. The differences are not clearly known.

Due to the quick and thorough "taming" of the virgin prairie only limited information about the plants or the animals present at the time of settlement was recorded and /or collected. More recent information gives general information about butterflies only interacting with the prairie. Irwin and Downey (1973), in a pioneering annotated checklist of the distribution of Illinois butterflies referred to a general lack of records from northwest and central Illinois, except for detailed reports from Mercer and Rock Island counties in the northwest, and Peoria, Mason and Jersey counties in the center of the state (Adams 1968). Butterflies in west-central Illinois counties close to or bordering the Mississippi River 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, distribution of individuals and the general butterfly plant preferences for the areas. However, the counties between the two areas previously mentioned have not been studied extensively.

This study observed species diversity, abundance, and habitat distribution of butterflies, forbs and grasses in four of the northwest central counties of the state. Observations, time of day and weather conditions were made once every two weeks along a specific route through the remnant and restored prairies. The purpose was to analyze the gathered observations with a sort program on a Macintosh SE/30 and derive the significant aspects of butterfly distribution in the prairies. This 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 and community similarity will be discussed in this paper.

METHODS

Observations

Field notes, photographs, and observations of butterflies were taken for the entire growing season from May 6 to October 15, 1988 and from May 11 to September 16, 1990 during the day light hours. Butterflies were netted only when necessary to prevent the possibility of handling effect (Morton 1984). Species were noted along with the date, location of capture and any plant association. Butterflies were identified according to Irwin and Downey (1973), Pyle (1981), Scott (1986), Shull (1987), Heitzman and Heitzman (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 included the time of day using a twenty-four hour clock and the weather conditions. This included whether it was sunny, partly cloudy, or raining. An approximation of the wind in such degrees as calm, light, or strong was made. In 1988 the temperature was measured on site with a Celsius thermometer. However, in 1990 the temperature was taken in degrees Fahrenheit from the Local Climatological Data monthly survey from Peoria, Illinois (1990). Other data such as rainfall and humidity were also taken from this source. These factors were recorded to see if they might have any effect on the activity, or diversity of the butterflies.

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 (Knox County) is a 0.3 ha piece of remnant prairie that has local preservation status supported by the cemetery board and managed by Knox College. The center of the cemetery, where the gravestones are located, was mowed but the edges were undisturbed. The east side is determined by a gravel road and the north by a grassy waterway consisting of imported grasses which then stretch to the north. Within the plot are four large oak trees and a rich assemblage of prairie forbs and grasses. In 1988 this cemetery was surrounded on the west and south by a clover field but in 1990 a cornfield was present.

Spring Grove Cemetery (Warren County) is a 0.4 ha Illinois Nature Preserve. It includes grasses with a small amount of forbs. No trees are present in the slightly rolling plot, except for two small wild cherry trees. The east side included an area of imported grasses which were mowed periodically, with a gravel road on the south side. A cornfield was on the west and north sides in both 1988 and 1990.

The Brownlee Cemetery (Mercer County) is a 0.8 ha Illinois Nature Preserve. This area is in the middle of flat farm land with a gravel road on the west side. The plot includes both a forb rich remnant and an adjoining five year old restored prairie plot. The remnant on the north side includes mostly forbs and a few short grasses. The southern restored prairie included forbs, a few tall grasses, lambs quarters, and foxtail grass in 1988. In 1990 the lambs quarters and foxtail were in sharp decline and the prairie forbs and grasses were increasing. The north and east sides were enclosed by corn in 1988 and soybeans were on the south side. In 1990 the field was again enclosed by soybeans and corn.

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 and contained four large coniferous trees. To the south is a forested area of deciduous and coniferous trees separated from the cemetery by a dirt road. In 1988 government oats grew on the west and north sides and corn on the east. Corn grew on the three sides in 1990.

The Knox College Biology Field Station (Knox County) includes 20 ha of restored prairie with oak and hickory forests at the surrounding edges. This prairie was established during the 1950's and 1960's when the original farm land was reseeded with prairie grasses and forbs. It is a well established tallgrass prairie with many of the more important prairie forbs represented. The prairie can be subdivided into three sections: an east, west, and south prairie. The east prairie is close to a lake and forest. The west prairie is also bordered by forest, but it is further from the lake. The south prairie is farthest from the lake and is also bordered by forest. The east and west sections had been burned in the spring of 1988 but the south section had not. The east and west prairies contained a wide variety forbs ranging from prairie to weedy plant species. In 1990 only the east and the eastern side of the west prairie were burned.

Data Treatment

Because of the lack of previous statistical data from other sources, the results compared to outside results can only be comparative in nature. Observations were entered into a sorting program on a Macintosh SE/30. Statview 521 was used on data when there were enough numbers of specific butterflies and plant species observed to make any statistical data relevant. Comparisons were made between 1988 and 1990 data. Community similarity was addressed using the similarity coefficients of the Jaccard index and the Sorenson index.

RESULTS

Species Present

The different species of butterflies found during the 1988 and 1990 season are listed in Table 1. The generic names are from Butterflies of West Central Illinois (Sedman and Hess 1985). Only the more common butterflies species were found. The more rare endemic prairie species, such as the arogos skipper, were not seen.

In 1988 and 1990 approximately one-third of the butterflies listed were seen one to three times in the entire season. While the skippers (Hesperidae) and Lycaenidae were almost exclusively in this group in 1988, the skippers were the predominant group in 1990, except for the silver-spotted skipper.

Table 1. Observed butterflies - 1988 and 1990.

Family Papilionidae	
* Eastern Black Swallowtail	*Papilio polyxenes* (Fabricius)
* Yellow Tiger Swallowtail	*Pterourus glaucus* (Linnaeus)
Family Satyridae	
* Little Wood Satyr	*Megisto cymela* (Cramer)
0 Olympian Wood Nymph	*Cercyonis pegala olympus* (Edwards)
Family Hesperoidea	
* Broken Dash	*Wallengrenia egeremet* (Scudder)
0 Byssus Skipper	*Problema byssus* (Edwards)
* 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)
0 Little Glassy Wing	*Pompeius verna* (Edwards)
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* (Latreille)
0 Wild Indigo Dusky Wing	*Erynnis baptisiae* (Forbes)
0 Zabulon Skipper	*Poanes zabulon*(Boisduval and LeConte)
Family Pieridae	
* Cabbage White	*Artogeia rapae* (Linnaeus)
Checkered White	*Pontia protodice* (Boisduval and LeConte)
* Clouded Sulfur	*Colias philodice* (Godart)
0 Little Sulfur	*Eurema lisa* (Boisduval and LeConte)
* Orange Sulfur	*Colias eurytheme* (Boisduval)
Family Lycaenidae	
* Coral Hairstreak	*Harkenclenus titus* (Fabricius)
* Eastern Tailed Blue	*Everes comyntas* (Godart)
Edward's Hairstreak	*Satyrium edwardsii* (Saunders)
Gray Hairstreak	*Strymon melinus humuli* (Harris)
0 Great Copper	*Gaeides xanthoides dione* (Scudder)
0 Hickory Hairstreak	*Satyrium caryaevorous* (McDonough)
* Spring Azure	*Celastrina ladon* (Cramer)
Family Nymphalidae	
0 American Painted Lady	*Vanessa virginiensis* (Drury)
0 Buckeye	*Junonia coenia* Hubner
Gray Comma	*Polygonia progne* (Cramer)
* Great Spangled Fritillary	*Speyeria cybele* (Fabricius)
0 Hackberry	*Asterocampa celtis* (Boisduval and LeConte)
* Painted Lady	*Vanessa cardui* (Linnaeus)
* Pearl Crescent	*Phyciodes tharos* (Drury)
* Question Mark	*Polygonia interrogationis* (Fabricius)
* Red Admiral	*Vanessa atalanta rubria* (Fruhstorfer)
0 Red-Spotted Purple	*Basilarchia arthemis astyanax* (Fabricius)
0 Silvery Checkerspot	*Charidryas nycteis* (Doubleday)
Family Danaidae	
* Monarch	*Danaus plexippus* (Linnaeus)

* species present both years (23)
0 species present only in 1990 (36)

Over the season thirty species were found in 1988 compared to thirty-six in 1990. However only twenty-three of the same species were actually present both years (Table 1). Seven of the species found in 1988 were not found in 1990. They included the dun skipper (*Euphyes vestris metacomet* Harris), the northern cloudy wing (*Thorybes pylades* Scudder), southern cloudy wing (*Horybes bathyllus* Smith), the checkered white (*Pontia protodice* Boisduval and LeConte), Edward's hairstreak (*Satyrium edwardsii* Saunders), the gray hairstreak (*Strymon melinus humuli* Harris), and the gray comma (*Polygonia progne* Cramer). In 1990, thirteen new species were observed (Table 1).

The Knox restored prairie showed an increase in five species from 1988. Munson showed an increase of one. Brownlee and Spring Grove lost two species while Copley's number of different species remained the same, however the same species were not present both years in all sites. There was a change in species present from 1988 to 1990.

Table 2. Species present in all sites.

1988	1990
Cabbage butterfly	Cabbage butterfly
Common Sulfur	Common Sulfur
Eastern Tailed Blue	Eastern Tailed Blue
Monarch	Monarch
Common sooty Wing	Orange Sulfur

In a site comparison of butterfly species in 1988 five species of butterflies were present in all sites (Table 2). They included the common sooty wing (*Pholisora catullus* Fabricius), the cabbage butterfly (*Artogeia rapae* Linnaeus), the clouded sulfur (*Colias philodice* Godart), the eastern tailed blue (*Everes comyntas* Godart) and the monarch. Five species were also present in all sites in 1990. The orange sulfur (*Colias eurytheme* Boisduval), the cabbage butterfly, the clouded sulfur, the eastern tailed blue and the monarch were present in all sites. The clouded sulfur, the cabbage butterfly, the eastern tailed blue and the monarch were present both years in all the sites but the common sooty wing was replaced by the orange sulfur. In 1990 the common sooty wing was found in only two remnant sites, Brownlee and Copley. The orange sulfur was found only in Brownlee and Munson and the Knox College restored prairie in 1988. For the most part the clouded sulfur, the eastern tailed blue, and monarch showed increases in individuals at all sites between 1988 and 1990. The cabbage butterfly remained in low numbers at all sites except for Knox in 1990.

Individuals Present

Numerically there were almost twice the number of individual butterflies overall, 1538 in 1990 compared to 783 in 1988

Table 3. Comparison by site of total population and species for 1988 and 1990.

Sites	Knox restored	Brownlee remnant	Munson remnant	Copley remnant	Spring Grove remnant	Total
Site size	20 ha	0.8ha	1.2 ha	0.3 ha	0.4 ha	
1988						
individuals	384	184	113	62	40	783
species	28	19	14	14	10	30
1990						
individuals	749	322	328	94	45	1538
species	33	17	15	14	8	36

(Table 3). In a site-to-site comparison all areas showed an increase in individuals. The largest increase was at Munson Cemetery with almost three times the number of individuals compared to 1988. The Knox College Biological Field Station and Brownlee Cemetery almost doubled in the number of individuals. Copley showed a small increase while Spring Grove showed only a very slight increase.

Community Similarity

The previous data gives only a limited look at the changes in species and individuals present between the two years. One of the easiest ways to measure the diversity in pairs of different sites is by the use of similarity coefficients. Two of the most useful are the Jaccard index and Sorenson index which can be used to measure the similarities of two sites over time and space. They are as follows:

Jaccard $SCj = c/ A + B - c$
Sorenson $SCs = c/ 1/2 A + B$

Here c equals the number of species found in both sites. A equals the number of species at site A with B the number of species in site B. The values can range from 0 when no species are found in both communities to 1, when all species are found in both communities or when there is complete similarity. A similarity coefficient matrix was calculated for each index comparing one site with another and then the remnant with restored sites for both years. The Jaccard index is based on the presence-absence relationship between the number of species in each community and the total number of species (Smith 1990). The Sorenson index differs from the Jaccard by measuring the ratio of the common to the average number of species in the two samples (Smith 1990). With the Sorenson index theoretically each species has an equal chance of being present in the two communities. It therefore gives greater weight to species present in both areas and less to species unique to either location and results in a greater similarity.

As can be seen from Table 4, when the restored prairie is compared to the total remnant the Jaccard index is 0.526 in 1988. The restored prairie was more like Brownlee, Munson and Copley. There is a low similarity of 0.266, 0.208, and 0.262 when Spring Grove is compared to the restored, Brownlee and Munson sites. Copley appears to be more similar than the other three areas to Spring Grove although the 0.412 value is the next highest value. Munson and Copley had the highest coefficient at 0.647.

In 1990 the Jaccard index between the restored and remnant rose to 0.639. The similarity values for Spring Grove (0.242) and Brownlee (0.316) and the restored prairie are low. However the Spring Grove and Copley similarity coefficients is the highest at 0.57. Between 1988 and 1990 the community likeness decreased in a comparison of all sites except for Brownlee, Munson, and Copley versus Spring Grove, Munson versus the restored, and in the comparison of the restored (0.526) to the total remnant (0.639).

The Sorenson index follows the same trends as the Jaccard index however the coefficients are higher in value (Table 5). The Sorenson index rose between 1988 and 1990 when the restored was compared to the remnant. The restored prairie in 1988 is most like Brownlee (0.723), Copley (0.553) and Munson (0.619). In 1990 low similarity values are indicated for Spring Grove (0.390) and Brownlee (0.480) and the restored prairie. However the Spring Grove and Copley value is the highest at 0.727.

Between 1988 and 1990 the community likeness decreased in a comparison of all sites except for Brownlee, Munson, and Copley versus Spring Grove, the restored versus Mun-

Table 4. Jaccard sites index for 1988 and 1990.

1988	Sites	Brownlee	Munson	Copley	Spring Grove	Total Remnant
	Restored	0.567	0.448	0.500	0.266	0.526
	Brownlee		0.571	0.434	0.208	
	Munson			0.647	0.262	
	Copley				0.412	
1990	Sites	Brownlee	Munson	Copley	Spring Grove	Total Remnant
	Restored	0.389	0.454	0.382	0.242	0.639
	Brownlee		0.391	0.348	0.316	
	Munson			0.450	0.353	
	Copley				0.570	

son, and in the comparison of the restored compared to the total remnant.

DISCUSSION

Since previous records of butterfly distribution in Knox, Warren and Henry counties are almost nonexistent the presence of butterflies in surrounding counties was used as an indication of butterfly presence in these areas. Because most of the habitat is similar for the areas, the distribution of butterflies should be the same for those who are strong fliers.

The twenty-three species seen both years were the more common butterflies. These butterflies are species that use a variety of food plants as adults, use plants found in many different habitats or are strong fliers. The presence or absence of the seven species from 1988 may or may not be significant. Due to the low number of individuals present one cannot tell if their disappearance is due to environmental factors such as presence or absence of specific larval or adult foods or to the chance they were just not observed. Some species of butterflies seem to be found in very low numbers most of the time. The thirteen new species of butterflies observed in 1990 may also be due to the same reasons because they were also found in low numbers of one to four individuals per species. The one exception is the Olympic wood nymph (*Cercyonis pegala olympus* Edwards) with a total of one hundred and five. It may be that this butterfly was confused with the little wood satyr (*Megisto cymela* Cramer) in 1988. However, the little wood satyr is much smaller and lighter in color and tends to be found around New Jersey tea when present on a site. Also no Olympic wood nymphs were captured in 1988 (Selser and Schramm 1988). Why the population came about is not known. However, some butterflies tend to undergo population explosions once every five to 10 years.

Looking at the species difference for the sites from 1988 to 1990 only Knox and Munson had an increase of five and one species respectively. No change was seen at Copley while a decrease of two species occurred at Brownlee and Spring Grove. One would expect an increase for all areas because of the increased rainfall. However, the lack of change at Copley and decrease at Brownlee and Spring Grove were interesting. These three areas may be too small or have less diversity in forbs and grasses and therefore, lack the ability to support more species.

Table 5. Sorenson sites index for 1988 and 1990.

1988	Sites	Brownlee	Munson	Copley	Spring Grove	Total Remnant
	Restored	0.723	0.619	0.667	0.421	0.690
	Brownlee		0.727	0.606	0.345	
	Munson			0.786	0.417	
	Copley				0.583	
1990	Sites	Brownlee	Munson	Copley	Spring Grove	Total Remnant
	Restored	0.560	0.625	0.553	0.390	0.780
	Brownlee		0.563	0.516	0.480	
	Munson			0.621	0.521	
	Copley				0.727	

The species found at all sites were expected because of their use of a variety of food plants as adults, the fact their food plant was found in a variety of habitats or present in sufficient quantity to sustain the population of butterflies present. These species also tend to have two or three broods over the year thus increasing their numbers quickly. When looking at the difference between the 1988 and 1990 eastern tailed blues it becomes apparent there was a population explosion (10 to 187). There was an increase at all sites including Copley, Brownlee and Spring Grove although they were smaller. The increase in eastern tailed blues may have caused interspecific competition at the Copley, Brownlee, and Spring Grove sites. They may have limited the number of species in this plot. Reasons for the decrease in common sooty wing may be due to the fact it was present in such low numbers in 1988 and just by chance alone it may have been missed in 1990. The orange sulfur may have been seen more in 1990 because of the increase in rainfall compared to 1988. These butterflies prefer alfalfa (Medicago), sometimes to the point of becoming pests (Heitzman and Heitzman 1987). The alfalfa was not as abundant and fields of it may not have been as close to the sites in 1988 as compared to 1990.

A comparison of the increase of individuals from 1988 to 1990 agrees with the Fourth of July Butterfly Counts Midwest Division (Opler and Brown 1988, 1990). The increase in individuals is probably due directly and indirectly to the increase in rainfall for 1990 and the more temperate weather (National Climatic Data Center 1990). 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 Fahrenheit or above (National Climatic Data Center 1988). The increased rainfall would allow for the more normal growth of forbs and grasses which provide sites for egg laying, perching for adults, and nourishment for fast growing larvae. The inflorescence would theoretically be of better quality and more abundant and therefore, provide more of the essential amino acids and sugars needed for adult survival so reproduction can take place and also migration, if needed. Hill (1992) demonstrated how temporal changes in the abundance of two lycaenid butterflies can be related to the adult food source.

It is possible some of the butterflies were counted more than once since each site was visited once every two weeks. However the more rare endemic butterflies have only one brood during a six week window of time during the entire season. It is therefore necessary to visit the sites on a regular basis because these windows vary either earlier or later from year to year. The endemic butterflies may have been at the remnant sites but none were found.

When the total population and species increases are compared, the Spring Grove site appears to be the poorest site with Knox, Brownlee and Munson being the best. This can be better addressed by the use of similarity coefficients. The Jaccard and the Sorenson indexes are based solely on presence (1) or absence (0) data. Therefore, they do not take into account the relative abundance of species. All species are equally represented whether they are rare or abundant (Smith 1990). This limits their usefulness but does give limited information about the similarities between the sites because of the butterfly species present.

Spring Grove appears to be the least like the other four sites when butterfly species are considered. The low coefficients are probably due to size of the site because a smaller area would be less likely to have enough of the variety or abundance of essential plants necessary for the successful rearing of the butterflies to the adult stage. Butterfly population numbers and species would therefore, be lower than at this site. There has also been a slow invasion of exotic grasses from the road way which might cause a decrease in numbers due to the loss of prairie habitat.

The restored site is more like Brownlee, Munson and Copley. Changes in indexes between the two years reflect the changes in species composition. However, with the larger number of species present in the Knox site the coefficients would not reflect a great similarity. The larger number of species at the Knox site would be expected because of its much larger size and its more diverse habitat. Most butterflies are very mobile and could fly in from different habitats to take advantage of the blooming prairie forbs. In a comparison of the remnant and the restored sites combined the coefficient is not much larger than for a single remnant site. So, it appears, each site is unique unto itself. No site is like the other. The restored site may or may not be equal to the remnant sites when butterflies are compared.

In a study dealing with creatures as mobile as butterflies it is hard to draw sharp conclusions. More information about the sites will be known when a comparison of the forbs and grasses present in each site is analyzed for both years along with the butterflies present. This may indicate some of the reasons for the differences in species of butterflies at each site. Only by continuing to monitor these sites over the next years, will information shed sufficient light on the intricacies of the relationships between the sites, their forbs, grasses and butterflies.

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PLAINS POCKET GOPHER SOCIAL BEHAVIOR

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Abstract. Social interactions of plains pocket gophers (*Geomys bursarius*) were studied by monitoring locations of radio-tagged individuals as they moved within their burrow systems. Gophers rarely came within 10 m of each other unless their home ranges abutted. This was determined by matching pairs of fixes obtained by radio-telemetry which were less than 30 minutes apart. However, gophers were aware of changes in surrounding home ranges as they investigated recently vacated home ranges within days of the disappearance of the resident gopher. Use of feces as "signposts" is suspected as one mechanism for sensing presence and reproductive status of a neighbor. Seismic vibrations from gopher digging and from their clicking vocalization are proposed as other mechanisms for detecting activities of neighboring gophers. Agonistic behavior was recorded by the tracking system more often than affiliative behavior. By the time juveniles were large enough to carry a transmitter, they had already dispersed. Seven intrusions into an occupied home range resulted in four displacements, one death, and two withdrawals. Den sites were defended from intruders. Agonistic behavior appears to be the mechanism which insures that each gopher has an adequate food supply.

INTRODUCTION

Pocket gophers have been characterized as solitary and highly territorial (Vaughan 1962). Caged gophers were fiercely intolerant of each other, with larger gophers killing or starving smaller animals (Howard and Childs 1959). Lack of sufficient detailed observations on behavior in the wild has led to the belief that pocket gophers defend their territories through combat (Hansen and Reid 1973). If death does not result from actual combat, the loser would probably withdraw to seclusion in its burrow system. Physical antagonism might also be a factor operating in the geographical separation of different species of gophers (Best 1973).

The burrow systems of pocket gophers have been described as being vigorously defended against intruders throughout most of the year, except during breeding season where plural occupancy of burrows was associated with a brief mating period (Miller and Bond 1960). Hansen and Miller (1959) reported 63 plural captures of 133 individual northern pocket gophers (*Thomomys talpoides*) in a total sample of 881 captures during breeding season. Adult females were together with young in 36.5 percent of those captures. Males with young were taken together 18.9 percent of the time and males together with females occurred in 13.5 percent of the captures (Hansen and Miller 1959). In three plural occupancies involving valley pocket gophers (*Thomomys bottae*), males burrowed into the tunnel system of adjacent females (Bandoli 1981). Howard and Childs (1959) conducted a study in which they removed trapped gophers during breeding season. Other gophers subsequently trapped in the same burrow system were always neighbors. Valley pocket gophers appeared to be polygamous in that male home ranges overlapped female home ranges, but males did not overlap other male home ranges and females did not overlap other female home ranges (Howard and Childs 1959).

Gophers live in a stable group in the sense they consistently encounter the same individuals as neighbors and they compete with these individuals for the same resources. Individual recognition is one of the basic components required for complex social behavior and implies prior experience with neighboring gophers. Howard and Childs (1959) conducted homing experiments and concluded gophers seem to be acquainted with neighboring burrow systems. The existence of relatively permanent deeper, larger tunnels may permit easy exploration of neighboring burrow systems. Howard and Childs (1959) found gophers utilizing existing burrow systems to return in homing experiments. They also found that opposite sex gophers had a limited penetration of tunnels across the outermost boundaries of their home ranges, but rarely found overlap in boundaries between gophers of the same sex. Thus, our working hypothesis was that there would be differences in frequency of encounter between same sex and opposite sex gophers.

METHODS

A population of free-ranging gophers on the Cedar Creek Natural History Area in east-central Minnesota was studied to determine whether there was contact between conspecifics. Radio transmitters were implanted (Zinnel and Tester 1991) in the body cavities of 37 individuals from October 1983 through September 1985. During this two year study, as many as six individuals were on the 50 x 50 m tracking grid at the same time. A micro-processor controlled monitoring system was able to locate one gopher every minute with a precision of 0.25 m (Zinnel 1992). Telemetry data for 22 pairs of gophers were sorted by date and time, and observations less than 30 minutes apart were matched.

Gopher interactions were summarized by examining the telemetry records for pairs of gophers and determining how

Table 1. Frequency of interactions between gophers. Telemetry fixes less than 30 minutes apart for opposite sex (A) and same sex (B) pairs of gophers were used to calculate statistics with respect to the Euclidean distance separating each pair.

A: Opposite Sex Pairs

First Gopher ID#	Second Gopher ID#	# ofObs <30 min Apart	Separation (Meters)					# of Obs <10 m Apart
			Avg.	S.D.	Min	Median	Max	
17	25	636	10.8	3.4	3	9	27	325
11	28	344	15.9	0.4	15	16	17	0
17	28	365	18.0	2.0	14	17	38	0
01	06	558	20.6	4.4	0	22	25	39
22	25	756	21.5	5.0	12	19	42	0
24	25	549	25.3	6.4	1	27	51	15
11	25	91	28.2	1.7	24	27	33	0
06	08	261	32.6	4.1	19	31	41	0
24	28	218	36.2	4.0	8	36	37	2
01	04	179	37.3	4.0	17	38	48	0
06	07	138	49.6	3.1	28	49	54	0

B: Same Sex Pairs

First Gopher ID#	Second Gopher ID#	# ofObs <30 min Apart	Separation (Meters)					# of Obs <10 m Apart
			Avg.	S.D.	Min	Median	Max	
25	28	156	13.1	1.8	9	12	27	4
01	02	330	17.2	13.3	0	19	50	102
07	08	95	22.6	5.3	15	22	52	0
22	24	409	24.0	5.0	10	23	36	0
17	24	529	28.0	4.9	6	28	39	10
11	17	361	28.6	0.9	22	28	31	0
17	22	997	29.9	4.9	6	27	47	1
01	08	634	37.0	5.8	15	34	47	0
01	07	238	40.9	11.1	11	46	49	0
11	22	20	41.4	3.1	37	40	46	0
11	24	150	52.1	0.3	51	52	53	0

often they were less than 10 m apart when the observations were less than 30 minutes apart. Using SPSS-X (Norusis 1988), the Euclidean distance in meters was calculated between each matched pair of fixes separated by the shortest time interval. Frequency histograms of separation distances and elapsed time were used to summarize interactions between pairs of gophers.

RESULTS

Neighboring gophers seemed to recognize when a den site and corresponding home range became vacant. Data from telemetry revealed six instances where a den site was investigated by another radio-tagged gopher within a few days of becoming vacant. In three of these cases, the investigating gopher took up residence. Gophers rarely were recorded as "close" to one another (Table 1). This may imply a mechanism for gophers to detect other gophers without physical contact. On seven occasions a gopher suddenly took up residence at a den site previously known to be vacant for at least two months. The transitions were usually abrupt, as determined by telemetry fixes, mound surveys, and trapping.

Within a home range, gophers vigorously defended den sites. Data from telemetry revealed seven instances where a radio-tagged gopher invaded an already occupied home range. In four of these situations, the resident gopher was displaced and in one case, killed. In the other two incidents, the gopher tracking system recorded what appeared to be conflict over a den site lasting several days. In these two cases, the resident

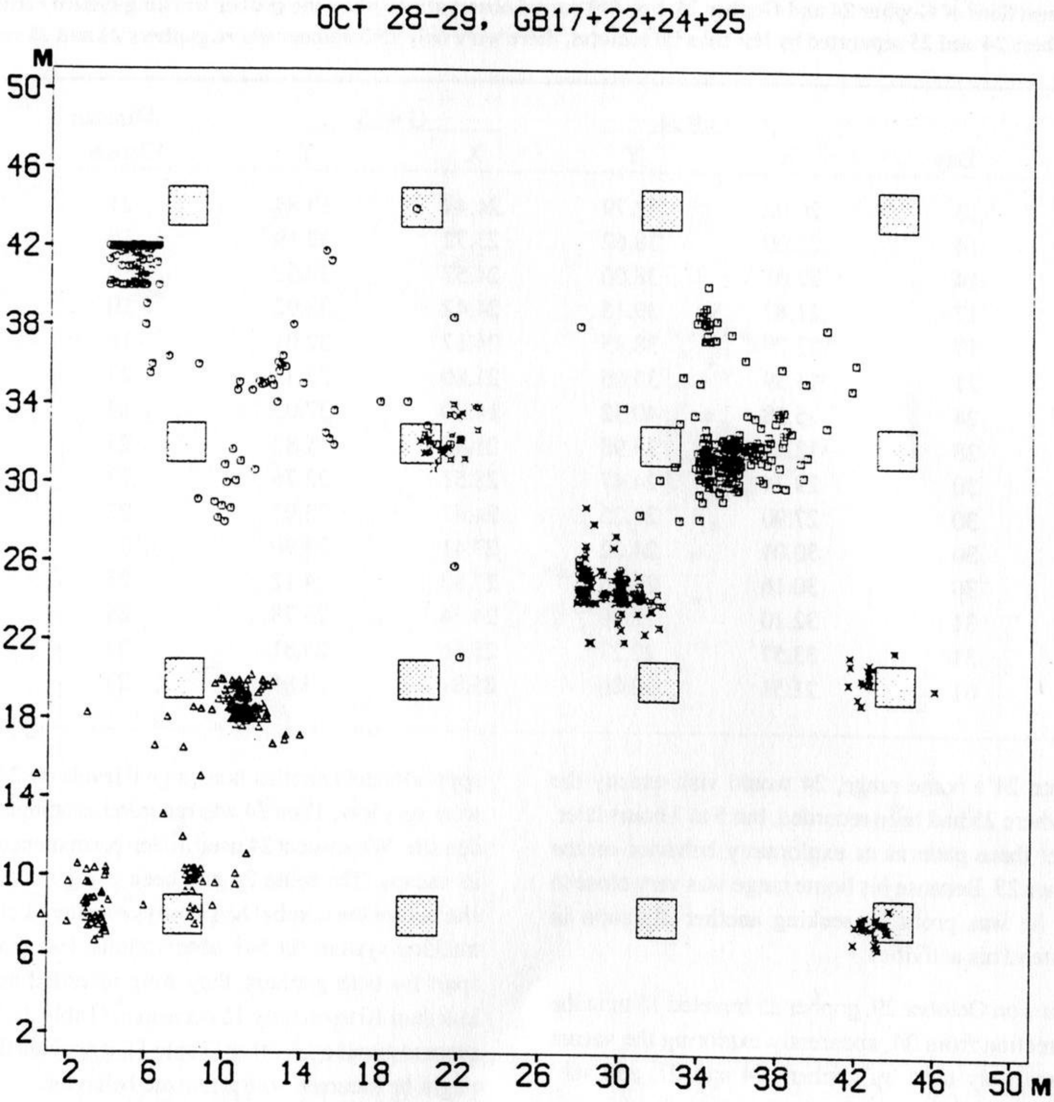

Figure 1. Gopher interactions on October 28 & 29, 1984. The 0.25 ha gopher tracking grid is indicated as a square outline. Tracking system coordinate labels are indicated in meters; the "interface zone" is approximately at X=22, Y=32 in this plot. There are 16 4 m^2 fertilized patches indicated as shaded squares. A square is the symbol for gopher 17, an x for gopher 25, a triangle for gopher 22, and an octagon for gopher 24.

gopher remained in possession of the den site. Details of one of these conflicts involve interactions of four gophers monitored by the gopher tracking system during October, 1984 (Figure 1). The principals were a large female (#24, 200g) and a small male (#25, 145g). The neighboring gophers were another large female (#22, 180g) and a small female (#17, 125g).

Data from telemetry revealed a discrete site centered around coordinates (24, 32) where fixes for different gophers appear in close proximity (Figure 1). This area will be referred to as an "interface zone" in the following discussion. We believe the burrow systems were interconnected in this region. Gophers 24 and 25 maintained a presence in this area, except for the last period, which was after their conflict. During the period from October 12 through 29, gopher 24 was recorded as being in this zone 48 times and gopher 25 was recorded 181 times. Gopher 17 also visited this area on two separate occasions. From October 12 through 23, gophers 24 and 25 were "close" to each other on only six occasions (Table 2) despite many individual fixes in this area. Generally, gopher 24 would visit the interface zone about three hours after 25 left. From October 24 through 28, gopher 25 intruded into the home range of 24 but they were never closer than 9 m, and were this close on only two occasions. When 25 started

Table 2. Interactions of Gopher 24 and Gopher 25. For 549 paired observations when the gopher tracking system recorded locations for gophers 24 and 25 separated by less than 30 minutes, there were only 15 instances where gophers 24 and 25 were less than 10 m apart.

		G # 24		G # 25			
Mo.	Day	X	Y	X	Y	Minutes Elapsed	Meters Separation
10	13	20.02	32.79	24.44	33.84	21	4.54
10	14	22.00	38.62	23.72	32.19	16	6.66
10	14	22.01	38.00	24.57	32.32	10	6.23
10	17	21.82	39.15	24.42	33.92	10	5.84
10	17	22.79	38.95	24.17	32.01	18	7.08
10	21	15.39	33.05	21.80	32.38	23	6.44
10	24	5.58	40.32	14.30	37.03	15	9.32
10	28	12.82	35.98	21.75	31.82	23	9.85
10	30	29.74	24.47	28.51	23.76	22	1.42
10	30	27.90	28.25	24.41	23.92	22	5.56
10	30	30.01	24.02	27.41	23.90	23	2.60
10	30	30.16	24.66	27.82	24.12	25	2.40
10	31	32.10	22.00	24.54	25.78	24	8.45
10	31	33.57	22.27	25.96	25.81	23	8.39
11	01	21.51	32.06	25.81	23.88	23	9.24

intruding into 24's home range, 24 would visit exactly the same area where 25 had been recorded, but 3 to 7 hours later. We interpret these patterns as exploratory behavior on the part of gopher 25. Because his home range was very close to gopher 17, he was probably seeking another direction in which to extend his activities.

At 1430 hours on October 29, gopher 25 traveled 15 m in the opposite direction from 24, apparently exploring the vacant den site previously used by gophers 04 and 07, and subsequently by 11 (Figure 2). As recorded by the tracking system, only 22 minutes elapsed from the time 25 left his den site until the time 24 arrived. It could have been less time because 22 minutes was the minimum time separating those two frequencies in the programming schedule. From October 29 through November 1, gopher 24 went to the den site belonging to gopher 25 several times while 25 was absent. Gopher 24 may have raided 25's food cache which was located 3 m away from the den. Gopher 24 made six trips back and forth between its den site and 25's cache in 17 hours, always taking the same path and traveling through the interface zone.

Around 0800 hours on October 30, gopher 25 returned to its den site. Telemetry fixes 22 minutes apart show 25 within 1.42 m of 24, who was at 25's food cache. We believe a fight may have occurred, maybe even on the surface, because the signal strengths doubled and the antenna pattern fluctuated wildly. This interaction lasted less than one hour because 25 was located back at its den site around 0900 hours. For approximately another hour, signal levels for 24's transmitter were very low. Then 24 was recorded as being back at its own den site. We suspect 24 used a deep permanent tunnel to make its escape. The route 24 had been using to return to its den site before the combat had always registered clearly with the tracking system. In 549 observations, less than 30 minutes apart for both gophers, they were recorded as separated by less than 10 m on only 15 occasions (Table 2). Since gophers seem to avoid each other (Table 1), it appears that a high cost might be incurred with agonistic behavior.

Affiliative interactions were inferred from manual telemetry fixes and trapping records. No interactions of this type took place in range of the tracking system. During breeding season, male gophers would stay close to, within 2 or 3 m, but not under the same tussock as the females. This was observed for three male-female pairs, one case with a male and two females, and one case with a male and three females. There were three instances where a male gopher relocated to be closer to females during the spring and summer, and then moved back to his previous home range for fall and winter. From manual observations on radio-tagged gophers, we believe males dug into adjoining female burrow systems to initiate reproductive behavior. On one occasion, we monitored a radio-tagged female away from her den site. We dug into the tussock to set a trap because her transmitter battery was almost dead. When we scooped out a shovel full of dirt, a male gopher was in the soil on the shovel.

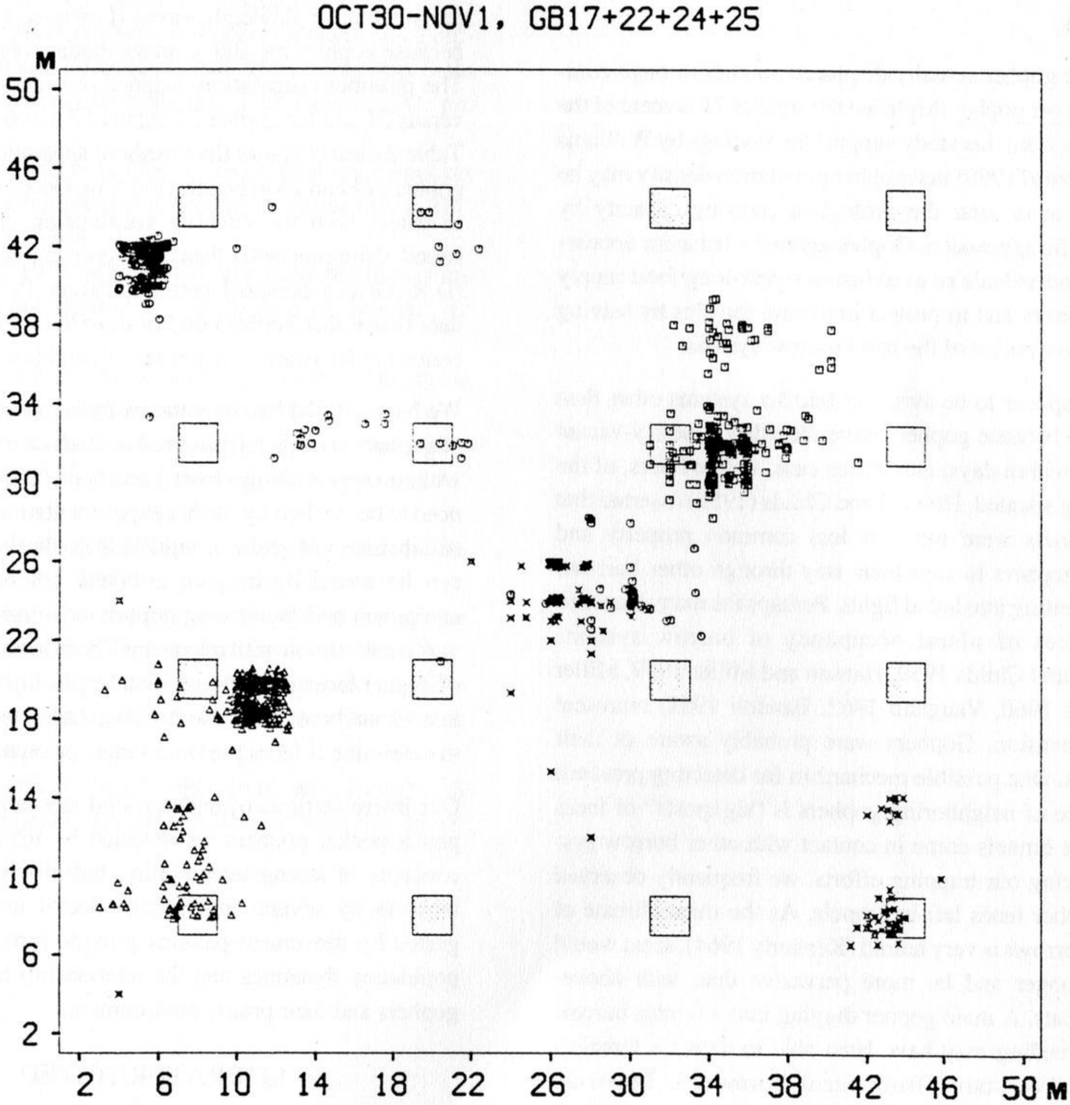

Figure 2. Gopher interactions from October 30 to November 1, 1984. The 0.25 ha gopher tracking grid is indicated as a square outline. Tracking system coordinate labels are indicated in meters; the "interface zone" is approximately at X=22, Y=32 in this plot. There are 16 4 m^2 fertilized patches indicated as shaded squares. A square is the symbol for gopher 17, an x for gopher 25, a triangle for gopher 22, and an octagon for gopher 24.

Juvenile gophers were determined to be the offspring of particular females on the basis of where the young gophers were initially trapped. The closest female which had been trapped while pregnant or lactating was assumed to be the parent. In nine of 16 cases, females relocated leaving female juveniles in possession of the natal burrow (Zinnel 1992). In the other seven instances, juveniles dispersed into nearby vacant home ranges. All three male juveniles dispersed.

DISCUSSION

Most of the detailed examples of gopher interactions recorded by telemetry were agonistic. Gophers were rarely recorded as being close to each other. Even during breeding season, males were never found in the same nest chamber with females, although males relocated closer to females. After raising a litter, more than 50 percent of adult females relocated, leaving female offspring in possession of the natal den site. All of these factors support the idea that gopher agonistic behavior has evolved to ensure an adequate food supply. However, we cannot rule out the possibility that agonistic behavior of males is related to defense or guarding of females.

When one gopher actually displaced another through combat, the larger gopher displaced the smaller 71 percent of the time. Data from this study support the findings by Williams and Cameron (1990) that gopher population density may be regulated at or near the ecological carrying capacity by intraspecific aggression. Gopher agonistic behavior appears to space individuals so as to insure a year-long food supply for both sexes and to protect immature females by leaving them in possession of the natal burrow system.

Gophers appear to be aware of burrow systems other than their own because gophers were recorded at newly-vacant den sites within days, and in one case, within hours, of the sites being vacated. Howard and Childs (1959) asserted that some tunnels were more or less common property and allowed gophers to find their way through other burrows without getting into lethal fights. Perhaps the many recorded occurrences of plural occupancy of burrow systems (Howard and Childs 1959, Hansen and Miller 1959, Miller and Bond 1960, Vaughan 1962, Bandoli 1981) represent rapid reinvasion. Gophers were probably aware of their neighbors. One possible mechanism for detecting presence or absence of neighboring gophers is "signposts" of feces left where tunnels come in contact with other burrow systems. During our trapping efforts, we frequently observed fresh gopher feces left in tunnels. As the microclimate of gopher burrows is very humid (Kennerly 1964), scent would remain longer and be more pervasive than with aboveground scats. A male gopher digging into a female burrow during breeding may have been able to detect a female's reproductive status from fecal hormones. Maternal pheromones present in the soft feces, caecotrophe, of rats have been found to mark mother and nest (Albone 1984). Similar processes might operate in equally coprophagous gophers.

Another possible mechanism for detecting presence is substrate vibrations which could be sensed by the long stiff hairs on the face and wrists, or by the long guard hairs and naked tail which help the gopher navigate when moving backwards through tunnels (Chase et al. 1982). Gophers make a loud clicking sound, easily transmitted by the packed soil because the intensity of low frequency sounds (<200 Hz) falls off more slowly in a burrow than in open air (D. R. Griffin pers. comm. 1985).

Based on measurements made on a variety of moist soils, Lewis and Narins (1985) found frog thump signals typically merged with the seismic background at distances of 3 to 6 m from the origin of the thumping. Vibrations from gopher digging or clicking vocalization probably would be detectable at distances of 6 m, the maximum distance for the propagation of Rayleigh waves (Lewis and Narins 1985), because gophers are able to make louder sounds than frogs. The minimum separation distance recorded for gopher 17 versus 24 and for gopher 22 versus 17 was 6 m (Table 1B). Table 2 clearly shows the threshold separation distance for gophers 24 and 25 to be just over 6 m. Geophones were able to detect both the clicking vocalization and "shushing" sound of digging better than microphones placed in a burrow (D.R. Griffin personal communication 1985). Telemetry data reveal that gophers do not have to come into physical contact to be aware of activities of neighboring gophers.

We have offered two hypotheses for the observed behavior of gophers sensing the presence or absence of other gophers without approaching closer than 6 m. These suggestions need to be verified by further experimentation. The function of substrate-born seismic signals in gopher communication can be tested by burying remotely controlled playback equipment and monitoring gopher movements in response to seismic stimuli with telemetry. The informational content of gopher feces could be verified by placing fecal signposts in a vacant home range during August/September dispersal to determine if feces presence deters occupancy.

Our interpretations of underground movement patterns of plains pocket gophers, as revealed by telemetry, support concepts of strong territoriality, but also indicate use of burrows by several individuals. Social interactions suggested by movement patterns provide further insight into population dynamics and the relationship between pocket gophers and their prairie environment.

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THE OCCURRENCE OF MYCORRHIZAS IN PRAIRIES: APPLICATION TO ECOLOGICAL RESTORATION

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Abstract. This paper aims to summarize data on the mycorrhizal status of prairie species, provide a general knowledge of mycorrhizal fungi, and discuss the relevance and potential role of mycorrhizal fungi in ecological restoration of grasslands. Mycorrhizal associations were documented both from a field survey of prairie species and from published studies reporting the mycorrhizal status of prairie species. Only those published studies examining more than three samples of a species are reported. Plants, including members of the Poaceae, Asteraceae, Fabaceae, Plantagonaceae, Scrophulariaceae, Asclepiadaceae, Onagraceae, Malvaceae, Commelinaceae, and Cactaceae, were collected in Illinois, Kansas or Oklahoma. Of the 109 species (25 families) surveyed or reported in literature, 96% were mycorrhizal and all formed exclusively arbuscular mycorrhizal associations. No family therefore was consistently non-mycorrhizal. The role that mycorrhizas play in reclamation, restoration, and structuring of plant communities and soil, and maintaining and promoting of plant species diversity, is believed to be important. Factors which directly or indirectly determine the occurrence of mycorrhizal propagules, for example, agricultural practices, disturbances and the presence or absence of mycotrophic and non-mycotrophic species, are potentially important in subsequent plant establishment. Restoration projects should take into account soil abiotic and biotic changes, especially those associated with mycorrhizal fungi, which can influence plant population response, competition, and ultimately successional trajectories. Given the high occurrence of mycorrhizas in prairies, it is clear that mycorrhizal fungi may play an important role in these communities, and warrant detailed study and incorporation into the practice of ecological restoration.

INTRODUCTION

Mycorrhizal infections or mycorrhizas represent one example of a plant-fungal association found under a range of abiotic conditions and habitats (for recent in depth reviews on mycorrhizal fungi see Safir 1987, Allen 1991, Brundrett 1991, Allen 1992). Specifically a mycorrhiza involves a symbiotic association of a host plant root and its associated fungus. Mycorrhizal fungi are believed to be important to plants in all ecosystems, however, restoration and management practices of prairies have, in general, not been concerned about their potential role in the establishment and maintenance of plant species or soil structure. Restoration efforts, however, have provided significant insights into the functional role of mycorrhizas, such as the role these fungi play in increasing soil aggregation (Miller 1987). The lack of interest in mycorrhizal fungi is partly the result of several factors including the inconspicuous nature of soil biota and below-ground processes, the scarcity of scientific studies addressing questions directly related to mycorrhizae, the absence of detailed studies on many prairie plants, and the difficulty in working with mycorrhizas (Miller 1987, Allen 1991). This paper aims to summarize data on the mycorrhizal status of prairie species, provide a general knowledge of mycorrhizal fungi, and discuss the relevance and potential role of mycorrhizal fungi in ecological restoration of grasslands.

Mycorrhizal fungi belong to the Basidiomycetes, Zygomycetes or Ascomycetes classes of fungi, and are divided into four groups according to the external and the internal morphology of the root-fungus association. The first group, arbuscular mycorrhizal (AM) fungi (previously called vesicular-arbuscular mycorrhizal, VAM, fungi), penetrate the root forming specialized structures. These are associated mostly with herbaceous and some woody species. The second group, Ectomycorrhizae (ECM), form dense hyphal networks, called Hartig nets, outside the roots and are associated almost entirely with woody species. The third group, the Ericaceous group, form both external and internal hyphal structures associated with roots, and are associated with members of the Ericaceae. The fourth group, Orchidaceous fungi, form structures internal to the root and are generally seed-borne. These are associated with members of the Orchidaceae family. The arbuscular mycorrhizal type, the most common mycorrhizal fungi associated with herbaceous plants, will be the focus of this paper.

Arbuscular Mycorrhizal (AM) Fungi

Arbuscular mycorrhizal (AM) fungi are presumably found associated with most of the world's herbaceous species (Newman and Reddell 1987). For example, eighty-nine percent of 61 plant families surveyed in arid and semi-arid regions world-wide were found to be mycorrhizal, with 84% of these families forming exclusively AM fungal associations (Dhillion and Zak 1993). Typically non-mycorrhizal taxa include Crucifereae, Zygophylaceae, Cactaceae, Chenopodiaceae, Cyperaceae, and Junaceae, although some species belonging to these families appear on occasion to be infected by mycorrhizal fungi under certain conditions (Newman and Reddell 1987, Safir 1987). At present, only a few studies have attempted to estimate the occurrence of mycorrhizas among prairie plants (e.g. Wetta 1972, Dickman et al. 1984, Medve 1984, Zajicek et al. 1986). To document the presence of mycorrhizas in prairie plants, we surveyed published records and examined several species in Illinois, Kansas and Oklahoma.

Nearly 160 species of AM fungi within six genera are currently recognized (Schenck and Perez 1990). Mycorrhizas are highly evolved, symbiotic associations between AM fungi and plant roots. AM fungal hyphae penetrate the root epidermis and exist as specialized structures (arbuscules, pelotons, vesicles and inter- and intracellular hyphae) in the root cortex. Arbuscules are dichotomous, highly branched structures which presumably are the sites of exchange between the host and the fungus. In mutualistic associations, the host plant receives inorganic nutrients and water in exchange for carbohydrates. The host plant is generally considered the sole source of carbohydrates for the fungus. External to the root, the fungus forms hyphae and reproductive bodies called chlamydospores or azygospores, which may rarely form in the root cortex as well. AM fungi are currently best identified at the species level by their characteristic spores. The fungal hyphae extend beyond the root hair zone and exploit nutrient rich regions and thus bridge regions near the root that are relatively deficient in immobile nutrients to more nutrient-rich regions not otherwise available to the plant. Mycorrhizal hyphae, like fine roots and root hairs, have important characteristics for the uptake of nutrients such as absorbing power for ions in solution, abundance and distribution, and an effective radius. The fungi thus function as a supplemental root system for the plant and increase the volume of soil that would normally be available for nutrient extraction to the plant (Jackson and Caldwell 1989, Friese and Allen 1991a). The beneficial effects of mycorrhizae are often associated with low availability of inorganic nutrients, especially phosphorus and nitrogen. The mycorrhizal hyphal network when well ramified through the soil could be important in competing with other organisms, including non-mycorrhizal roots, for nutrients and moisture (Harley and Smith 1983). Mycorrhizal hyphal bridges can also link the circulatory system of plants of similar and different species and, therefore, may influence succession and community dynamics (Newman 1988, Friese 1991, Friese and Allen 1991a). The number of species studied is small and the ecological significance unknown, but mycorrhizal links have been reported between annuals, herbaceous perennials, and tree species as well as between different taxonomic groups (Newman 1988, Brundrett 1991, Friese and Allen 1991a). The role that mycorrhizas play in structuring plant communities is thought to be important because it operates through processes such as plant competition, phenology and interspecific nutrient transport through hyphal links both intra- and inter-specifically (Allen and Allen 1984, Newman 1988, Allen and Allen 1990, Gange et al. 1990, Brundrett 1991).

Plant Responses to AM Fungal Infection

Growth responses of temperate plants, especially grasses, to mycorrhizal infection are varied, ranging from mutualistic to parasitic (e.g. Hetrick et al. 1988, Allen et al. 1989, Anderson and Liberta 1989). In general, plants benefiting from the mycorrhizal association have greater tolerance to drought stress and higher photosynthetic rates, biomass production and inorganic nutrient uptake than non-mycorrhizal plants of the same or other species. The type of response observed in mycorrhizal plants can depend on one or several factors, including available soil moisture, inorganic nutrient availability, substrate pH, type of AM fungal species, type of host plant root system, plant host species, age of host plant, time of year, irradiance and soil associated microorganisms (e.g. Harley and Smith 1983, Fitter 1985, Anderson and Liberta 1992, Dhillion 1992a, Dhillion 1992b). Although increased biomass production has very often been used as an indicator of the nature of AM symbiosis, it is not always the best measure of the degree of host responsiveness or dependency on mycorrhizae, since physiological dependency on AM has been suggested, at least for some grasses (Allen and Allen 1986). The plants that appear to benefit from AM are those that have a rather coarse root morphology, produce few root hairs and occur in low nutrient habitats (Baylis 1976, Anderson and Liberta 1987). Baylis (1976) and Fitter (1991), for example, suggested that grasses that can persist without AM (non-mycorrhizal or facultative) generally have a well developed, fine, and highly branched topology.

Many studies on effects of mycorrhizas on plants have been done in controlled environments (green houses and growth chambers) and on crop plants. Growth habit and physiology of crop plants, however, are quite different from those of native or wild plants (Grime 1979, Chapin 1980), and most likely mycorrhizal fungi effect these plants differentially. Therefore, it is important to use care in drawing parallels between crop plants and native plants. To date little work has been conducted on non-crop forbs.

Ecological specificity

In field studies several plant species have been shown to exhibit host-endophyte preference or 'ecological specificity' when associated with indigenous mycorrhizae. The degree of plant-AM preference, measured as infection and sporulation levels and/or fungal morphology, has been related to plant dependence on native AM species (Giovannetti and Hepper 1985, Henkel et al. 1989, McGonigle and Fitter 1990, Dhillion 1992a, Dhillion 1992b, Sanders and Fitter 1992). For example, when little bluestem (*Schizachyrium scoparium*), prairie dropseed (*Sporobolus heterolepis*) and big bluestem (*Andropogon gerardii*) grasses were inoculated with each of three AM species, each formed mycorrhizas with all three AM fungal species. However, based on infection and sporulation levels there was apparently greater preference for different AM species by each plant (Dhillion 1992a, Dhillion unpublished data). These results suggest that although, mycorrhizal fungi are nonspecific in their selection of host species, it is possible that, a host exposed to a mixed selection of AM fungi could be preferentially infected by one or more of the endophytes. This specificity may affect the success of using non-native seed in restoration efforts. In a recent study, little bluestem plants from Kansas when grown in soil from Illinois experienced growth depression (Anderson and Roberts 1993). Anderson and Roberts (1993) attributed the lack of a positive mycorrhizal response for little bluestem to the lack of compatibility between Illinois sand prairie AM fungal endophytes and plants grown from Kansas seed source. The successful establishment of native seedlings thus may be determined by the presence of appropriate native mycorrhizal fungal species and *vice versa.*

Plant and Mycorrhizal Reponses

Fire

Grassland fires can directly affect the abundance of soil surface microflora (e.g. Wicklow 1975, Kapustka and Rice 1976). For mycorrhizae, however, recent studies on little bluestem grass (*Schizachyrium scoparium*) in Illinois sand prairies have shown that mycorrhizal dynamics, as well as soil microbial populations and saprophytic fungi may, in fact, be indirectly affected more by the host plant's response to fire than directly by fire (Dhillion et al. 1988, Dhillion and Anderson 1989, Dhillion and Anderson 1993a, Dhillion and Anderson 1993b, Dhillion and Anderson 1993c).

Biocides

Many management practices utilize biocides to control weeds, pests and pathogens. Although specific results differ, in conjunction with high application rates of fungicides and herbicides, both adversely affect mycorrhizal survival and function. Fungicides grouped either as substituted aromatic hydrocarbons used to control pathogens like *Alternaria* spp., *Fusarium* spp., *Rhizoctonia* spp., *Phythium* spp, [e.g., botran, lanstan and quintozene (PCNB)], or as benzimidazole fungicides such as benomyl thiophanatate, carbendazim, thiophanatate, all used as seed treatments, soil drenches, and foliage sprays, both inhibit AM fungi (Nemec 1980, Habte et al. 1990). In contrast, two anti-oomycete fungicides, fosetyl and metalaxyl, when applied at low levels are frequently known to stimulate AM colonization (Afex et al. 1991, Hetrick and Wilson 1991).

Fertilizers

Numerous studies suggest that different AM fungi may each be adapted to a specific fertility level suggesting that increased fertilization may be more deleterious to AM fungi indigenous to infertile soils than to AM fungi indigenous to fertile soils (Hayman 1982, Dehne 1987, Johnson and Pfleger 1992). Therefore, runoff from agricultural fields that reaches a prairie may have a detrimental effect on mycorrhizal infection or spore production although it may provide nutrients for prairie species.

Grazing

Both grazers and mycorrhizal fungi depend on plants for energy thus an interaction seems likely. The response of mycorrhizal plants to grazing by vertebrates and invertebrates vary from no response to stimulation in both growth and physiological conditions. Generally plants respond to moderate grazing by increasing biomass allocation to growth below the grazing zone, particularly enhanced tillerage and root growth, and to altered growth habit (Miller 1987). Heavy grazing by ungulates, however, reduced mycorrhizal activity (Bethlenfalvay et al. 1985, Wallace 1987) and altered species composition in rangeland (Bethlenfalvay et al. 1985). Alternatively, grazing increased AM fungal colonization in shortgrass prairie (Davidson and Christensen 1977) and in savanna (Wallace 1981). In addition to indirect responses to surface grazers, mycorrhizal fungi are directly affected by soil grazes. Invertebrates (e.g. amoeba, nematodes, mites, collembola and earthworms; see review by Fitter and Sanders in Allen 1992) are heavy grazers on mycorrhizal fungal hyphae. Despite the contradictions in responses to grazers, animals serve as important agents in the dispersal and migration (soil enrichment) of mycorrhizal fungi (Allen 1991, Dhillion et al. 1994, McGinley et al. 1994).

Drought

Mycorrhizal fungi can cause changes in plant water relations and can, in many cases, improve drought resistance or tolerance. Most host changes related to water relations are likely to be secondary responses due to improved nutrition. For an excellent in-depth review on drought and mycorrhizas see Safir (1987).

Soil Structure

The presence of AM hyphae can improve soil conditions. In studies of a chronosequence of restored prairie at Fermi National Laboratories, Chicago, soil aggregation was shown to be related to the presence of AM hyphae associated with roots of prairie plants (Miller and Jastrow 1990). Physical entanglement by roots and the hyphae of mycorrhizal fungi is considered to be a major mechanism in the binding of microaggregates into macroaggregates, thereby bringing about the recovery of the crumb structure of degraded agricultural soils (Miller and Jastrow 1986, Miller 1987, Miller and Jastrow 1990, Miller and Jastrow 1992). Miller and Jastrow (1990) have hypothesized that changes in the proportions of aggregates of various sizes and the amount of water-stable aggregates could be used as an index of disturbance, or recovery, in the restoration process.

Disturbance and Species Interactions

Plant communities are dynamic assemblages of species, in which all species should be viewed as potential invaders and colonists (e.g. Grubb 1977, Grime 1979, Pickett and White 1985, Gross 1987). Periodic or occasional disturbances and the type of disturbance, both large and small scale, can remove some species and allow others to become established for a certain time. In grassland and other communities, animal mounds can become sites of enhanced plant establishment because of both improved nutrient status and the presence of beneficial mycorrhizal fungi capable of initiating a mutualistic association with the invading plants (e.g. Allen, M. 1988, Dhillion et al. 1994, McGinley et al. 1994). Thus mycorrhizal plants, associated with animal disturbances, may have a better chance of establishment than nearby non-mycorrhizal individuals. Disturbance can also effect the species composition of the mycorrhizal fungus community, which can result in shifting of dominant fungal species and thereby changing host response and composition (Miller 1979). Understanding how communities develop following a small or large scale disturbance is fundamental to developing an understanding of the maintenance and restoration of diversity in plant communities (Grubb 1977, Mooney and Gordon 1983, Gross 1987, Allen E. 1988, Dhillion et al. 1994).

METHODS AND MATERIALS

Plants surveyed for this study were collected from Illinois, Kansas or Oklahoma (Table 1). Five to ten individual plants of each species were examined. Feeder roots (generally 2 mm diameter) were used for mycorrhizal evaluation. When roots could not be processed immediately they were fixed in formalin-acetic acid-alcohol (FAA; 10:35:10:5 formalin-water-ethanol-acetic acid) as soon as possible after excavation. Roots fixed in FAA were washed at least three times prior to placement for clearing in a glass vial with 10% KOH and left for about 5 days at room temperature. [Roots may be directly put in KOH if staining is to be done fairly soon, thus eliminating the FAA step. However this step can be hastened by heating root in the vial at 90°C in a water bath between 15 - 25 mins.] Cleared roots were rinsed three times with water and acidified with 1% HCl. The roots are left in 1% HCl for at least 5 mins. The HCl was decanted off and 0.5 % trypan blue stain in lactoglycerol (lactic acid:glycerol:water; 1:1:1) added to cover the roots. The roots were left in the stain for about 5 days or heated in a water bath at 90°C for about 15-30 mins. The trypan-blue-lactoglycerol solution was decanted and lactoglycerol solution added (without stain). This destaining removed excess stain, and preserved roots for up to a year. Prairie herbaceous species do not contain much lignin and thus do not require any drastic clearing processes. However, if such a requirement should arise, consult Schenck (1982) and Norris et al. (1992).

The staining procedure removes the cellular contents of the roots leaving fungal structures which appear blue when viewed under the microscope. Root fungi other than AM fungi were also stained by this process. The presence of structures characteristic of AM fungi (arbuscules, pelotons, vesicles, and coenocytic hyphae) were used to separate from other root endophytes. Percent AM colonization (% infection) was estimated using the gridline intersection method (Giovannetti and Mosse 1980).

In addition to collections made for this study, data used include those from published studies reporting on the mycorrhizal status of plant species. Only those published studies which examined at least three individuals of a species are reported in this study.

RESULTS AND DISCUSSION

Mycorrhizal Status of Prairie Plants

Like plants in other communities (Moore 1987, Dhillion and Zak 1993), prairies also consist of a large number of mycorrhizal species. Of the 109 species (25 families) surveyed in this study or reported in literature, 96% were mycorrhizal and all formed exclusively AM associations (Table 1). It should be noted that in members of families considered to be non-mycorrhizal, mycorrhizas were seen, on occasion, to form although infection levels were very low (ranging from 1-5%). No family therefore was consistently non-mycorrhizal. In this study, dominant prairies grasses, such as big bluestem, little bluestem, and Indian grass (*Sorghastrum nutans*), were found to be highly mycorrhizal. Generally plants which tend to form coarse or tap roots [e.g. rigid goldenrod (*Solidago rigida*), bull thistle (*Cirsium vulgare*), Jerusalem artichoke (*Helianthus tuberosus*), Indian grass, big bluestem] also were highly mycorrhizal. In contrast,very fine rooted plants [e.g. hairy aster (*Aster pilosus*), daisy fleabane (*Erigeron annuus*), three-awned grass (*Aristida oligantha*), grama grasses (*Bouteloua* spp.), large fescue (*Festuca arundinacea*), and foxtails (*Setaria* spp.)] had low levels of infection. These fine rooted plants may be better able to exploit soil resources then coarse rooted ones, and thereby not require a

Table 1. Mycorrhizal status and infection levels of prairie species of North America. Infection levels (% I) may be low (L, <15 %), moderate (M, 15-40 %),high (H, >40 %)[1] or absent (N).

FAMILY AND SPECIES	COMMON NAME	HABITAT	% I
APOCYNACEAE			
Apocynum cannabinum	Dogbane	oldfield	M
ASCLEPIADACEAE			
Asclepias syriaca	Prairie Milkweed	oldfield	L
Asclepias tuberosa	Green Milkweed	sand prarie, forest	M
Asclepias viridiflora	Butterfly weed	sand prairie	M
ASTERACEAE			
Ambrosia artemisiifolia	Common Ragweed	sand prairie	M
Ambrosia trifida	Giant Ragweed	sand prairie	M
Antennaria neglecta	Pussy toes	sand prairie	M
Artemisia ludoviciana	Western Mugwort	sand prairie	H
Aster drummondii	Drummond Aster	mesic prairie	M
Aster ericoides	Heath Aster	mesic prairie	M
Aster novae-angliae	New England Aster	mesic prairie	M
Aster pilosus	Hairy Aster	mesic prairie	L
Chrysanthemum leucanthemum	Ox-eye Daisy	roadside	L
Cirsium arvense	Canada Thistle	oldfield	M
Cirsium discolor	Field Thistle	oldfield	M
Cirsium undulatum	Wavyleaf Thistle	oldfield	L
Cirsium vulgare	Bull Thistle	roadside	M
Conyza canadensis	Horseweed, Muleweed	sand prairie	L
Erigeron annuus	Daisy Fleabane	mesic prairie	L
Erigeron philadelphicus	Philadelphia Fleabane	oldfield	L
Eupatorium perfoliatum	Common Boneset	oldfield	M
Helianthus annuus	Common Sunflower	roadside	H
Helianthus grosseserratus	Sawtooth Sunflower	roadside	H
Helianthus mollis	Downy Sunflower	oldfield	M
Helianthus rigidus	Prairie Sunflower	mesic prairie	M
Helianthus sempervirens		mesic prairie	H
Helianthus tuberosus	Jerusalem Artichoke	oldfield	H
Hieracium pratense	King of Devils	roadside	L
Lactuca biennis	Tall Blue Lettuce	oldfield	M
Liatris spicata	Dense Blazing Star	prairie	H
Rudbeckia hirta	Blackeyed Susan	sand prairie	M
Silphium integrifolium	Rosinweed	roadside	H
Silphium laciniatum	Compass Plant	oldfield	H
Silphium perfoliatum	Cup Plant	roadside	M
Silphium terebinthinaceum	Prairie Dock	roadside	H
Solidago altissima	Tall Goldenrod	oldfield	L
Solidago canadensis	Canada Goldenrod	oldfield	L
Solidago graminifolia	Grass-leaved Goldenrod	oldfield	N
Solidago juncea	Early Goldenrod	sand prairie	L
Solidago rigida	Rigid Goldenrod	mesic prairie	H
Solidago speciosa	Showy Goldenrod	mesic prairie	H
Sonchus asper	Spiny Sow Thistle	mesic prairie	L
Taraxacum officinale	Common Dandelion	oldfield	M

Table 1, continued.

FAMILY AND SPECIES	COMMON NAME	HABITAT	% I
Tussilago farfara	Coltsfoot	oldfield	M
Vernonia fasciculata	Ironweed	dry-mesic	M
CACTACEAE			
Opuntia humifusa	Prickly-pear Cactus	sand prairie	M
CHENOPODIACEAE			
Chenopodium album	Lamb's Quarters	roadside	L
COMMELINACEAE			
Tradescantia ohioensis	Spiderwort	mesic prairie	L
Tradescantia virginiana	Spiderwort	sand, mesic prairie	M
CORNACEAE			
Cornus racemosa	Gray Dogwood	oldfield	L
EUPHORBIACEAE			
Acalypha rhomboidea	Three-seeded Mercury	mesic prairie	M
FABACEAE			
Baptisia lactea	White Wild Indigo	dry-mesic prairie	H
Cassia fasciculata	Partridge Pea	mesic prairie	H
Lathyrus palustus	Marsh Vetching	mesic prairie	M
Tephrosia virginiana	Goat's Rue	sand prairie	M
Trifolium pratense	Red Clover	mesic prairie	L
Trifolium repens	White Clover	mesic prairie	L
LABIATAE			
Lycopus uniflorus	Northern Bugle Weed	mesic prairie	M
Prunella vulgaris	Self-heal	mesic prairie	M
LOBELIACEAE			
Lobelia inflata	Indian Tobacco	mesic prairie	M
OENOTHERACEAE			
Oenothera biennis	Evening Primrose	mesic prairie, roadside	M
OXALIDACEAE			
Oxalis stricta	Yellow Wood Sorrel	mesic prairie	M
PLANTAGINACEAE			
Plantago lanceolata	Buckhorn	mesic prairie	H
Plantago major	Common Plantain	mesic prairie	H
Plantago rugelii	Rugel's Plantain	mesic prairie	H
POACEAE			
Agropyron repens	Quack Grass	oldfield	N
Andropogon gerardii	Big Bluestem	mesic prairie	H
Aristida purpurascens	Purple Triple-awned	sand prairie	L
Aristida oligantha	Three-awned	sand prairie	L
Bouteloua curtipendula	Side-oats Grama	sand prairie	M
Bouteloua dactyloides	Buffalo Grass	dry prairie	L
Bouteloua gracilis	Blue Grama	dry prairie	L

Table 1, continued.

FAMILY AND SPECIES	COMMON NAME	HABITAT	% I
Bouteloua hirsuta	Hairy Grama	dry-mesic prairie	M
Bromus inernis	Awnless Brome	oldfield	N
Digitaria sanguinalis	Crab Grass	mesic prairie	L
Elymus canadensis	Nodding Rye	mesic prairie	M
Elymus cinerus		mesic prarie	H
Eragrostis spectabilis	Tumble Grass	sand prairie	H
Eragrostis trichodes	Sand love Grass	sand prairie	H
Festuca arundinacea	Large Fescue	oldfield	L
Koeleria pyramidata		oldfield	L
Lolium perenne	English Rye Grass	mesic prairie	L
Panicum capillare	Witch Grass	sand prairie	M
Panicum lanuginosum		sand prairie	M
Panicum virgatum	Switch Grass	sand prairie	L
Paspalum stramineum	Sand Paspalum	sand prairie	M
Phleum pratense	Timothy	mesic prairie	L
Poa pratensis	Kentucky Bluegrass	prairie	L
Schizachyrium scoparium	Little Bluestem	sand,mesic prairie	H
Setaria geniculata	Perennial Foxtail	mesic prairie	M
Setaria glauca	Yellow Foxtail	mesic prairie	L
Setaria faberii	Giant Foxtail	oldfield	M
Setaria lutescens	Yellow Foxtail	oldfield	L
Sorghastrum nutans	Indian Grass	mesic prairie	H
Spartina pectinata	Prairie Cordgrass	mesic prairie	H
Sporobolus heterolepis	Prairie Dropseed	mesic prairie	H
Stipa spartea	Porcupine Needlegrass	prairie	L
POLEMONIACEAE			
Phlox pilosa	Downy Phlox	prairie, oldfield	M
POLYGALACEAE			
Polygala senega	Senega Snakeroot	dry-mesic prairie	
Polygala verticillata	Whorled Milkwort	dry prairie	L
POLYGONACEAE			
Polygonum persicaria	Lady's Thumb	mesic prairie	N
Rumex acetosella	Sour Dock	mesic prairie	N
POLYPODIACEAE			
Onoclea sensibilis	Sensitive Fern	mesic prairie	L
MALVACEAE			
Abutilon theophrastii	Velvet Leaf	mesic prairie	M
ROSACEAE			
Potentilla simplex	Common Cinquefoil	mesic prairie	M
Prunus serotina	Wild Black Cherry	oldfield	M
Rubus allegheniensis	Common Blackberry	oldfield	M
Rubus hispidus	Swampy Dewberry	oldfield	M

Table 1, continued.

FAMILY AND SPECIES	COMMON NAME	HABITAT	% I
SCROPHULARIACEAE			
Linaria vulgaris	Butter-and-eggs	mesic prairie	L
Verbascum thapsus	Common Mullien	mesic prairie,roadside	M
SOLANACEAE			
Physalis heterophylla	Ground Cherry	mesic prairie	M
Solanum carolinense	Horse-Nettle	prairie	M
UMBELLIFERAE			
Daucus carota	Wild Carrot,Queen Ann's Lace	oldfield,roadside	N
VITACEAE			
Vitis sp.	Wild Grape	oldfield	M

[1]These data are a list of prairie species collected in either Illinois, Kansas, Oklahoma (Dhillion, period of collection 1987-91) or summarized from Anderson and Liberta 1987, Dickman et al. 1984, Ebbers et al. 1987, Hetrick et al. 1986, Hetrick et al. 1990, Medve 1984, Medve 1985 and Zajicek et al. 1986.

heavy investment in a symbiotic association. Another explanation may be that even highly mycorrhizal species can have differential responses to AM fungal infection due to soil nutrient levels, soil microbes and ecotypic variation (Hetrick et al. 1986, Cerligione et al. 1988, Hetrick et al. 1988, Anderson and Liberta 1989, Anderson and Liberta 1992, Meredith and Anderson 1992).

Relevance and Potential Role of Mycorrhizal Fungi in Restoration

Ewel (1987) stated that the success of community restoration can be judged by five criteria, sustainability, invasibility, productivity, nutrient retention and biotic interactions, all of which should be critically investigated and not simply based on whether or not a reconstituted community appears to resemble the original. Many restoration attempts are designed to establish the relatively high level of species diversity, species composition and interactions characteristic of a prairie community (Kline and Howell 1987, Dhillion et al. 1994). Successful restoration should be ecologically sustainable and repeatable. Much of what we understand today about restoration is, however, anecdotal because of the past lack of emphasis on collecting and analyzing data. This has made repeating successful restorations difficult (Allen E. 1988, Allen 1991). Thus for a prairie to be truly ecologically sustainable the need to understand interactions of its various components becomes essential. With the current rapid loss of species and deterioration of our ecosystems restoration efforts have increased. It is necessary for successful restoration to obtain appropriate data for past efforts including investigating less obvious habitat factors, such as mycorrhizal fungi, prior to the implementation of restoration, and subsequent management practices (Allen E. 1988, Allen 1991, Dhillion et al. 1994).

Species Diversity, Plant Community and Succession

There is also growing evidence from both laboratory and field data suggesting that AM fungi may be important in maintaining and promoting plant species diversity since the diversity of AM fungal communities has been correlated to diversity of plant communities (Rabatin and Stinner 1989, Allen 1991). Mycorrhizas for example can increase plant diversity in early successional communities (Gange et al. 1990). Non-mycotrophic species (those that do not form mycorrhizas) exist in early successional communities where AM fungal inoculum is low or absent and mycotrophic species predominate where AM fungal inoculum is high (Miller 1987, Allen 1989, Allen 1991). Thus a highly diverse community of AM fungi may be desirable to increase options for host-fungus combinations. Plant dependency on mycorrhizae may change with the successional stage of the system (Miller 1987, Allen 1991). For example, in shrublands of the western U.S., many pioneer herbaceous plants of early succession belong to non-mycorrhizal families, whereas late successional stages have plants belonging to mostly mycorrhizal families (Allen 1991). It appears that the earlier seral stages have facultative species that, through various means, build inoculum and nutrient levels that facilitate the establishment of obligate mycotrophs (Allen and Allen 1986, Allen 1989). In prairie restorations, Howell and Jordan (1991) argue that poor competitors should be planted first to facilitate their establishment before aggressive plants, perhaps pioneer species, are introduced. It is very likely that these 'poor competitors' or 'conservative species', which are regarded by some workers as late seral successional species

(Howell and Jordan 1991, Allen 1992, Howell personal communication), may successfully establish only when appropriate AM fungi are present. It is not surprising that some late successional species do not establish in disturbed environments where AM inoculum may be very low or absent (Janos 1980, Allen E. 1988, Allen 1992).

Numerous studies have suggested that the mycorrhizal inoculum levels (mycorrhizal propagules) of soils determine plant species establishment and persistence, and introduction of soils from late successional seres may hasten the rate of reclamation or restoration (Allen E. 1988, Allen 1991). The increasing number of species dependent on AM and larger number of mycorrhizal species in later seral stages along with growth and physiological responses of plant species from different seral stages provide support for this hypothesis (Allen E. 1988, Allen 1991). The type of mycorrhizal community found on a site, therefore, may influence the next assemblage of species through its affects on the mycorrhizal fungus population (Friese and Allen 1991b). One management strategy is to hasten the rate of succession by planting late seral species in the hope that the vegetation and associated abiotic and biotic components will continue in the same trajectory of succession as would the undisturbed system (Allen E. 1988). This approach, however, may be futile if needed AM fungi are absent from the establishment site. It is logical, therefore, to hypothesize that the introduction of AM fungi may facilitate continuity in succession and thus hasten the restoration process (Moorman and Reeves 1979, Janos 1980).

AM Fungal Inoculum

Mycorrhizal hyphae in root fragments can be more effective inoculum than spores. Recent studies show that mycorrhizal hyphae in root pieces are probably the most important source of inoculum (mycorrhizal propagules) since mycorrhizal root fragments can initiate infection faster than spores (Friese 1991, Friese and Allen 1991a, Friese and Allen 1993). Spores, however, can account for up to about 33% of the potential inoculum in sand prairies (Dhillion and Anderson 1993a, Dhillion and Anderson 1993c). The most significant contributor to mycorrhizal inoculum levels is, however, the presence of an intact mycorrhizal hyphal network and associated root system (Newman 1988, Friese and Allen 1991a). In general, mycorrhizal inoculum potential, and sporulation levels, are lowest in the middle of the growing season and highest near the end of the season (Dhillion and Anderson 1993). Seasonal patterns in sporulation can, however, vary according to the individual AM fungal or plant species. The presence of mycorrhizal propagules in recently removed soils has been shown to contain more viable mycorrhizal propagules than soils that have been stored (Miller 1984). The inoculum of AM fungi is reduced when soil is disturbed, such as during mining, biocide application, agricultural practices and erosion.

CONCLUSION

Given the high occurrence of mycorrhizas in prairies and the potential benefits of the mycorrhizal symbiosis, prairie restoration processes, plant establishment, community dynamics and soil development in prairie can be influenced by the presence or absence of mycorrhizal fungi. Factors which directly or indirectly determine the occurrence of mycorrhizal propagules, for example, agricultural practices, natural disturbances and the presence or absence of mycotrophic and non-mycotrophic species, are potentially important in subsequent plant establishment. Restoration projects should take into account soil abiotic and biotic changes, especially those associated with mycorrhizas which can influence plant population/community response, competition, and ultimately successional trajectories. Without successful establishment of appropriate mycorrhizal fungi, the plant species composition and soil characteristics of grassland communities undergoing restoration may be altered, and lead to the further degradation of these lands.

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EFFECTS OF POPULATION SIZE ON FERTILIZATION, SEED PRODUCTION, AND SEED PREDATION IN TWO PRAIRIE LEGUMES

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Abstract. Fragmentation of prairies has resulted in remnants with small populations which may be susceptible to local extinction. In this study, the effects of population size and density on flower fertilization, seed production, and seed predation were measured for eight populations of purple prairie clover (*Dalea purpurea*) and lead plant (*Amorpha canescens*) in Dickinson County, Iowa. In purple prairie clover, the number of flower stems in a population was significantly related to the percentage of flowers fertilized and percentage of seeds attacked, suggesting that small populations are less likely to attract pollinators or support seed predators. In lead plant, fertilization was high and seed predation low in all populations except the smallest one, suggesting that factors other than size affect pollination and seed predation. Population density did not affect the characteristics measured. These results indicate that fragmentation is affecting important characteristics related to population viability in some prairie forbs.

INTRODUCTION

Landscape fragmentation resulting from the destruction of natural ecosystems is a severe problem of global proportions (Robinson et al. 1992). Although all ecosystems have been impacted by fragmentation and much attention has been paid to this problem in temperate and tropical forests (Harris 1984), the most severe case of ecosystem fragmentation has occurred on prairies. Two hundred years ago, North American prairies were a contiguous biome extending north from Texas to the boreal forests of Manitoba and west from the deciduous forests of Indiana and Wisconsin to the Rocky Mountains (Weaver 1954). Today, all but a tiny faction of the prairie biome has been converted to use by humans. For example, Iowa had about 12.4 million ha of prairie (Hayden 1945), but today, only about 0.004% of this area (about 465 ha) is protected by the state in its preserve system.

When large, contiguous ecosystems are broken up into small, isolated remnants, the effects on biodiversity are devastating. The rate of species extinctions increases as remnant size decreases (MacArthur and Wilson 1963 and 1967, Glass 1981) and those species that survive have decreased probabilities of persistence (Shaffer 1981 and 1985, Soule 1983 and 1987). The causes of decreased viability of small populations are numerous (Gilpin and Soule 1986). First, inbreeding depression, genetic drift, and decreases in genetic variability may impair a population's ability to survive and reproduce and/or adapt to environmental changes. Second, demographic factors such as failure to successfully reproduce or recruit new individuals in the population may affect persistence. Third, environmental stochasticity resulting from natural catastrophes may alter the availability of important resources. In the case of plants, the occurrence of severe droughts may be critical. Lastly, interactions between local populations can affect gene flow and the probability of recolonizations following local extinctions.

Population viability analysis, which uses a probabilistic approach to the study of persistence, is the tool now being used to develop generalities about extinctions in order to preserve species diversity. However, to date, most population viability studies which have attempted to establish minimum population sizes necessary for the survival of a species have been conducted on large mammals or birds (Jones and Diamond 1976, Franklin 1980, Shaffer 1981, Soule 1987, Soule et al. 1988, Berger 1990). Far fewer studies of minimum population size have been conducted on plants (Menges 1990). Thus, our ability to develop generally applicable rules concerning viability of populations is greatly hindered (Murphy et al. 1990). In this study, I examine the effect of population size and density on reproductive effort and seed predation in two common prairie legume species, purple prairie clover [*Dalea purpurea* Vent. = *Petalostemon purpureus* (Vent.) Rydb.] and lead plant (*Amorpha canescens* L.). Specifically, I ask if population size, measured as the number of flowering stems, or population density has a significant impact on the percentage of flowers fertilized, percentage of seeds filled, or percentage of seeds attacked by seed predators.

METHODS

Natural History of Study Species

Lead plant is an erect semi-shrub, producing 1-10 flowering stems up to 1 m tall. It is common on undisturbed, upland prairies throughout the Great Plains from Texas to southern Manitoba and from Indiana to northwest Wyoming (Weaver 1968, McGregor et al. 1986). Flowers are produced in spike-like, terminal, compound racemes from May to August (July in Iowa). Principle pollinators are *Bombus* species and solitary bees (R.W. Cruden personal observation). Abscised flowers leave a visible scar. The one-seeded indehiscent pods are often attacked by the bruchid beetle, *Acanthoscelides submuticus* (Sharp) (R.W. Cruden personal observation). Damaged fruits, as well as those that are partially or completely filled remain on the infructescence until the time of dispersal in the fall. Fruits are dispersed passively by wind.

Purple prairie clover is a perennial herb with a distribution similar to lead plant (McGregor et al. 1986). It produces one to many aboveground shoots, 2-9 dm tall. Flowers are produced in terminal, dense cone-like or cylindrical spikes from June to August (July in Iowa). Fruits as well as unfertilized flowers do not abscise from the spike until the fall. Primary pollinators are *Bombus spp.* (R.W. Cruden pers. obs.). The one-seeded indehiscent pods are often attacked by the bruchid beetle, *Apion capitone* (Kissinger) (R.W. Cruden pers. obs.). Fruits are dispersed passively by wind.

Study Sites

Eight populations of each species located in Dickinson Co., Iowa were sampled in 1990. Populations of lead plant and purple prairie clover were sampled on the Cayler Prairie and Freda Haffner Iowa State Preserves. Cayler Prairie Preserve consists of approximately 65 ha of hills and swales of morainal origin (Aikman and Thorne 1956). The Freda Haffner Preserve consists of approximately 48 ha of similar terrain and is dominated by a large, steep-sided prairie pothole or "kettle" (Salisbury and Knox 1969). At both the Cayler and Haffner Preserves, large discontinuous patches of each species were sampled. Six additional lead plant populations were sampled in a privately owned hillside remnant prairie, and in five roadside sites. Six purple prairie clover populations were sampled in a restored prairie at Iowa Lakeside Laboratory and in five roadside sites.

Roadside populations of both lead plant and purple prairie clover occupied narrow strips of land from 3 - 10 m wide between the road and adjacent fields. No herbicide spraying was evident in any of these populations during the year of sampling. Populations within a species were at least 1.6 kilometres apart, except for two small, roadside populations of purple prairie clover separated by 0.8 kilometres.

Sampling Procedures

In the roadside populations of both species, the rectangular area occupied was measured and the absolute number of flowering stems were counted directly. Density was determined from these measurements. In non-roadside populations of both species, the perimeter of each population or patch was marked to determine the shape of the area occupied. Parallel transects of variable length were laid throughout the area occupied and the number of above ground flowering stems in regularly spaced quadrats along each transect was determined. A minimum of 100 quadrats per population were sampled. For lead plant, quadrat size was 1 m^2 and for purple prairie clover quadrat size was 0.5 m^2. Because purple prairie clover can produce many flowering stems from a single root system, the number of clumps of flowering stems in each quadrat were counted. The number of flowering stems was estimated by multiplying the number of clumps times the mean number of flowering stems/clump determined for a subsample of at least 25 clumps in each large population or patch. The size of the area occupied by each population was determined by simple geometry based on the lengths and distances between transects. Absolute population size, measured as the number of above ground flowering stems, was calculated from the density and area estimates.

In large populations of each species, 22-26 randomly chosen flowering stems were tagged and in small populations (fewer than 25 flowering stems) all stems were tagged. At maturity, one infructescence (raceme or spike) with undispersed seeds was collected from each tagged stem. In some populations, dispersal of seeds prevented collecting infructescences from all tagged stems. Fifty fruits from each infructescence were classified as filled (plump, well rounded seeds), not filled (dented, small seeds), unfertilized (no ovular development), or attacked by seed predators. In lead plant all fruits present on an infructescence were counted in order to estimate the number of flowers fertilized (see below). In purple prairie clover, an additional category of unopened flowers (anthers with pollen present) was ,used.

Due to the difficulty in directly counting the number of flower scars present on an inflorescence of lead plant, flower number was estimated as follows. In 1991, 29 inflorescences of lead plant that held mature flowers were collected from Cayler Prairie Preserve. On each inflorescence the number of flowers was counted. The length of each inflorescence axis was measured to the nearest mm and the diameter of the axis was measured to the nearest 0.1 mm. When the axis is considered as a cylinder, regression analysis indicated that the surface area of the inflorescence axis was an excellent predictor of the number of flowers produced ($F_{(1,27)}$ = 132.00, p 0.0001, adjusted $r^2 = 0.82$).

Statistical Analysis

Preliminary analysis revealed that the requirements for the use of parametric statistics (normality of data distribution and homogeneity of variances) were met. The maximum r^2 improvement stepwise multiple regression procedure (SAS 1979) was then used to examine the effects of absolute number of flowering stems in a population and population density on three dependent variables: percentage of flowers fertilized, percentage of fruits filled, and percentage of fruits attacked by seed predators. This procedure determines the one-and-two variable models producing the highest r^2. Density and number of flowering stems were not significantly correlated in either species ($p > 0.42$).

For purple prairie clover, flowers were considered fertilized if they were categorized as filled, not filled, or attacked by

Table 1. Absolute number of flowering stems and density (flowering stems/m^2) in sampled populations of A) purple prairie clover (*Dalea purpurea*) and B) lead plant (*Amorpha canescens*) in 1990.

Species and Populations	Number of Flowering Stems	Density
A) Purple prairie clover		
Haffner Preserve	16,028	30.76
Roadside remnant	2,095	4.07
Cayler Prairie	1,778	4.89
Roadside remnant	1,421	10.89
Restored prairie	642	4.12
Roadside remnant	243	39.99
Roadside remnant	87	20.71
Roadside remnant	57	27.80
B) Lead plant		
Private remnant	12,545	1.03
Cayler Prairie	11,707	0.67
Haffner Preserve	2,815	2.47
Roadside remnant	155	0.39
Roadside remnant	106	0.19
Roadside remnant	23	5.00
Roadside remnant	18	0.48
Roadside remnant	14	0.58

seed predators. For lead plant, the ratio of the total number of fruits to the estimated number of flowers was used as the percentage of flowers fertilized. All percentages were arcsin transformed prior to analysis. Means per population for each dependent variable were used in the regression analyses.

For lead plant, one-way ANOVA was used to determine if significant variation between populations existed in the dependent variables measured. In these analyses population was considered as a categorical variable. The Student-Newman-Kuels test (Zar 1974) was used to determine significant differences (if any) between populations.

RESULTS

Variation in the number of flowering stems was four orders of magnitude in the sampled populations of both purple prairie clover and lead plant (Table 1). Density of flowering stems in purple prairie clover varied about 10-fold in the populations sampled and about 26-fold in the lead plant populations.

Regression analyses using single variable models (Table 2A), show that in purple prairie clover $\log_{10}$ of the number of flowering stems in a population was significantly and positively related to the percentage of flowers fertilized (Figure 1A) and percentage of flowers attacked by seed predators (Figure 1B). Population size was not significantly related to the percentage of seeds filled. Inclusion of population density as a predictor in all regression models had an insignificant effect in all cases (all p values >0.70) and did not significantly improve r^2 values. In both purple prairie clover and lead plant, the percentage of flowers per inflorescence that were fertilized and the percentage of fertilized flowers setting fruit were unrelated to inflorescence size as measured by the total number of flowers (ANOVA, p >0.35).

In lead plant, significant variation in existed for the three dependent variables measured (ANOVA, all p values <0.01). The smallest roadside population with only 14 plants had significantly fewer flowers fertilized (Figure 1C), and and more seeds destroyed by seed predation (Figure 1D). In addition, the percentage of fruits filled in the smallest population (20%) was significantly less than in the other populations (40-84%). In regression analyses, neither $\log_{10}$ absolute number of flowering stems or population density significantly affected percentage of flowers fertilized, percentage of seeds filled, or percentage of seeds attacked by seed predators (Table 2B).

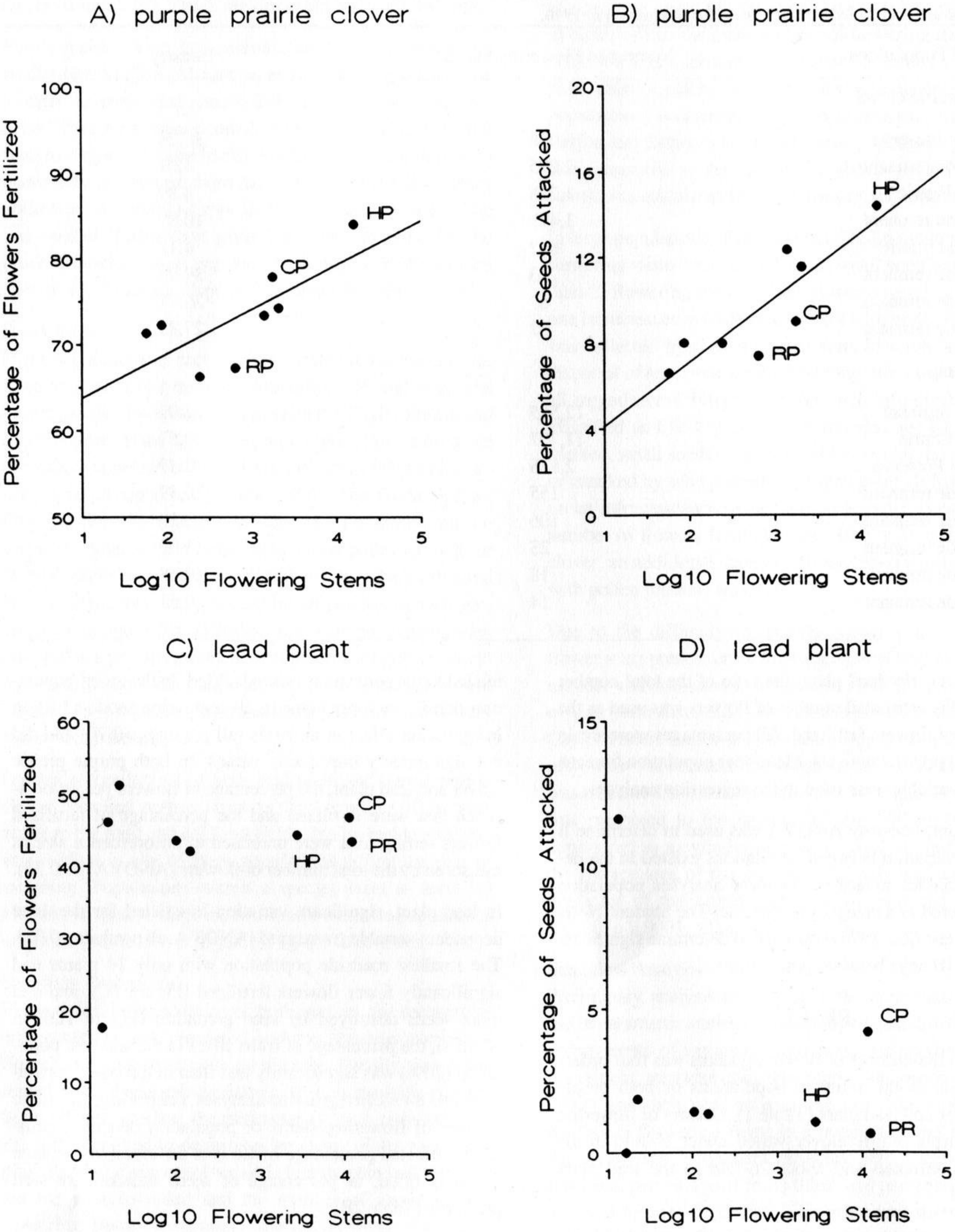

Figure 1. Effects of log10 number of flowering stems on percentage of flowers fertilized and percentage of seeds attacked by seed predators in purple prairie clover (A and B) and lead plant (C and D). HP = Haffner Preserve, CP = Cayler Prairie, RP = restored prairie, PR = private remnant. See results for statistical analyses.

Table 2. Results of regression models using $\log_{10}$ number of flowering stems in a population as predictors of percentage of flowers fertilized, percentage of fruits filled, and percentage of seeds attacked by seed predators. Degrees of freedom for all models was 1,6.

A) Purple prairie clover

Dependent variable	F	P<	r^2
% flowers fertilized	8.08	0.0295	0.574
% fruits filled	3.61	n.s.	0.376
% fruits attacked	10.33	0.0183	0.633

B) Lead plant

Dependent variable	F	P<	r^2
% flowers fertilized	1.70	n.s.	0.221
% fruits filled	0.04	n.s.	0.007
% fruits attacked	0.20	n.s.	0.033

DISCUSSION

This study indicates that for some prairie forb species ecosystem fragmentation is affecting characteristics associated with population viability. Conversion of prairie to farmland in Iowa has directly lead to reductions in the size of many populations of prairie species. In most instances, these populations now occupy small areas along roadsides, and they are usually isolated from other populations by relatively large distances.

In purple prairie clover, the percentage of flowers fertilized was directly related to population size (Figure 1A). The cause of reduced flower fertilization in purple prairie clover is likely related to the decreased ability of small roadside populations in degraded remnants to attract the necessary pollinators. In *Astragalus canadensis* (Platt et al. 1974), small, isolated clumps of plants had decreased pollination success compared to larger clumps. Similarly, Karron (1987) found that rare species of *Astragalus* were poor competitors for pollinators compared to more widespread congeners. However, it is also possible that reduced seed set in small populations is at least partially attributable to inbreeding depression because most species of prairie legumes are outcrossers (R.W. Cruden personal communication).

In contrast to purple prairie clover, the percentage of flowers fertilized in lead plant was consistent across nearly all population sizes. Although the smallest population sampled (14 flowering stems) had significantly lower flower fertilization than the remaining seven, it is unlikely that this is solely due to population size, given that two populations only slightly larger (18 and 23 flowering stems) had levels of flower fertilization equivalent to much larger populations. The reasons for the reduced flower fertilization in the smallest population are unclear.

Population size was also positively related to levels of seed predation in purple prairie clover, suggesting that viability of the seed predator population attacking this species is closely tied to plant population size. In many herbivorous insects, host plant population size is a critical factor affecting population size and indirectly, levels of damage (Pimentel 1961, Courtney 1982). However, in lead plant, seed predation was relatively low in all populations except for the smallest population which also had low flower fertilization, suggesting that population dynamics of this seed predator are controlled by factors largely unrelated to host plant population size. In general, the levels of seed predation in both purple prairie clover and lead plant found in this study were considerably lower than reported for other prairie legumes. For example, in both *Astragalus canadensis* (Platt et al. 1974) and *Baptisia* spp. (Haddock and Chaplin 1982, Evans et al. 1989) 60% or more of the seeds or pods were destroyed by pre-dispersal seed predation.

At present there is insufficient data to develop detailed analysis of population viability of prairie forbs in order to determine minimum viable population size. Critical information on demography is lacking, although the smallest populations of both species contain few non-reproductive individuals (S. Hendrix pers. obs.), suggesting that viability of these populations may be tenuous. However, it is likely that minimum population size for the prairie forbs examined falls within the range of 50-5000 individuals (Lande and Barrowclough 1987) found for other species.

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Renée Renaud 93

ROCKEFELLER PRAIRIE: A CASE STUDY ON THE USE OF PLANT GUILD CLASSIFICATION OF A TALLGRASS PRAIRIE

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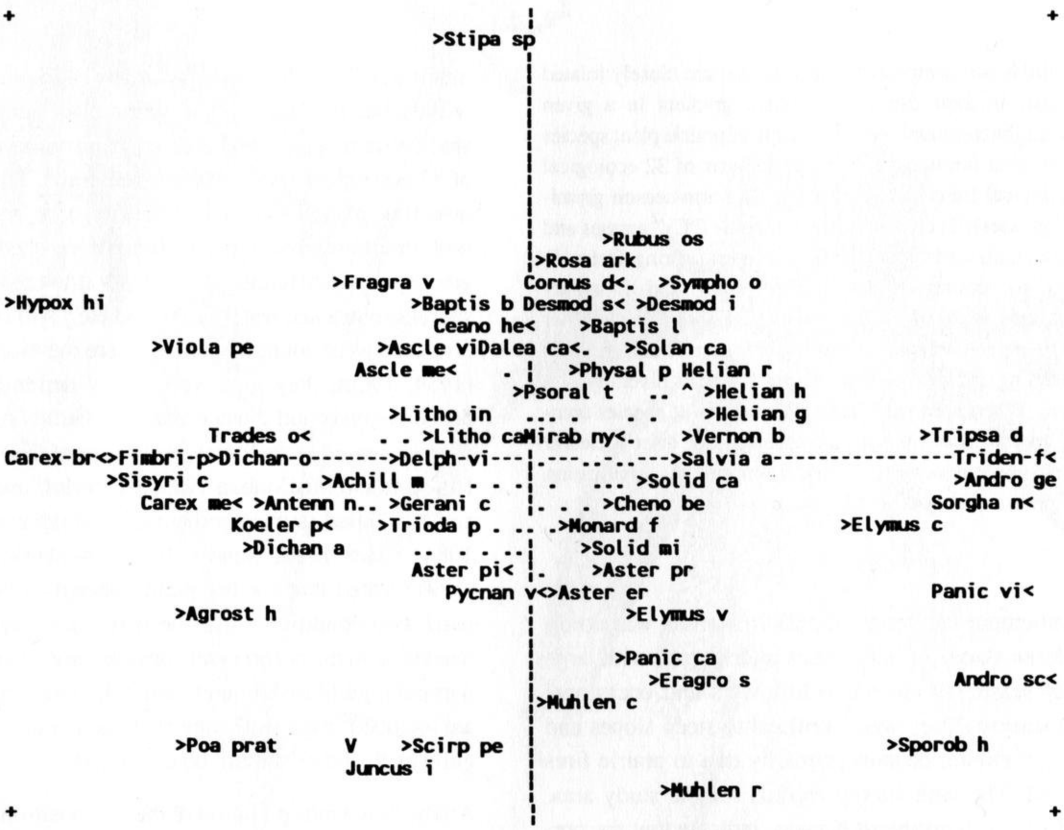
Abstract. Guilds are composed of species that are closely related to one another in their use of a resource gradient in a given community. Eight commonly-known guilds of prairie plant species have been verified through multivariate analysis of 32 ecological and morphological traits. The guilds are: 1) warm-season graminoids ("C_4" grasses); 2) cool-season graminoids ("C_3" grasses and sedges); 3) annuals and biennials; 4) ephemeral spring forbs; 5) spring forbs; 6) summer/fall forbs; 7) legumes; and 8) woody shrubs. This case study of the University of Kansas' Rockefeller Native Prairie demonstrates how these guilds can be a useful tool for understanding and interpreting the plant species diversity of a native prairie. When used with statistical analysis of species composition, it appears that the guild perspective can offer a clearer understanding of species composition and community classification of tallgrass prairie than traditional techniques.

INTRODUCTION

The pre-settlement landscape of eastern Kansas was dominated by dense stands of tall grasses interspersed with large numbers of seasonally showy wildflowers and occasional patches of shrubs. Trees were confined to steep slopes and the borders of stream courses primarily due to prairie fires (Wells 1970). The land survey records for the study area, Jefferson County in northeast Kansas, indicate that the pre-settlement vegetation was 95% prairie and only 5% forest (Kansas State Board of Agriculture 1881). Since then, there has been a dramatic change in the landscape with agriculture converting most lands to cropland. Today, only about 1 or 2% of the landscape in the study area has native prairie of high-quality as its vegetation (Lauver 1989).

The term guild has been defined by Root (1967) as a group of species that exploit the same class of environmental resources. He used this definition for different bird taxa that share the same or similar functional niche (e.g. guilds of leaf gleaners or bark gleaners.) Historically, the term guild was first used to describe groups of plants with similar lifestyles, and specifically four distinct guilds were named: lianes, epiphytes, saprophytes, and parasites (Schimper 1898). Guild is the literal translation of the German word *Genossenschaft* originally adopted by Schimper who used it in a sense similar to a medieval union of skilled craftsmen plying the same trade. The guild concept for plants usually have not been tied to resources as obviously as animal guilds have, perhaps because of the difficulty in reconciling plant diversity with notions that resource partitioning structures communities (Simberloff and Dayan 1991). In previous research (Kindscher 1991), the eight prairie plant guilds used in this study were proposed and verified using multivariate statistics of 32 ecological and morphological traits. These traits (representing plant habit, leaf characteristics, stem structures, root structures, and reproduction) were used because they give species different abilities to use environmental resources (nutrients, water, light, and etc.) Although the guilds proposed were not new, as many were mentioned by Weaver (1954, 1968), they were verified by detrended correspondence analysis and cluster analysis. Guilds of species have been discussed in the literature in terms of theory (Root 1967, Hawkins and MacMahan 1989, Simberloff and Dayan 1991) and as applied to management (Severinghaus 1981, Verner 1984, Szaro 1986, Reader 1988). Simberloff and Dayan (1991) stated that for the guild concept to be successfully used, two conditions must be met: 1) a clear statement is needed as to the criteria and considerations that have led to a particular guild assignment; and 2) if sympatric related biota are included in the study, the exclusion of one from the same guild as the other, should be explained.

Analysis and interpretation of the composition and quality of prairie remnants are often difficult. Through both vegetative sampling and traditional floristic analysis, a good understanding of the composition of a prairie can be obtained. When multivariate techniques are also included, particularly when species are grouped into guilds, a better interpretation of the area and its biodiversity may be achieved (Severinghaus 1981, Kindscher 1991, Grabherr 1989, Walker 1992). Besides determining which guilds of prairie species are present, the percentage of coverage for each guild can also be determined as can the ecological and morphological traits that are most important in determining each of these guilds. The analysis of the Rockefeller Native Prairie as a case study will demonstrate the value of these techniques for analyzing an individual prairie.



	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	.34	.26	.15	.11

Figure 1. First two axes of a detrended correspondence analysis of species positions from 32 morphological and ecological traits of 121 species on the Rockefeller Tract Prairie, and eigenvalues for the first four axes. Species names abbreviated (see Appendix 1 for abbreviations) and printed where space allows. Species located at arrows, which point to species abbreviations. Some arrows represent more than one species. Species too close together to print are marked with a ".".

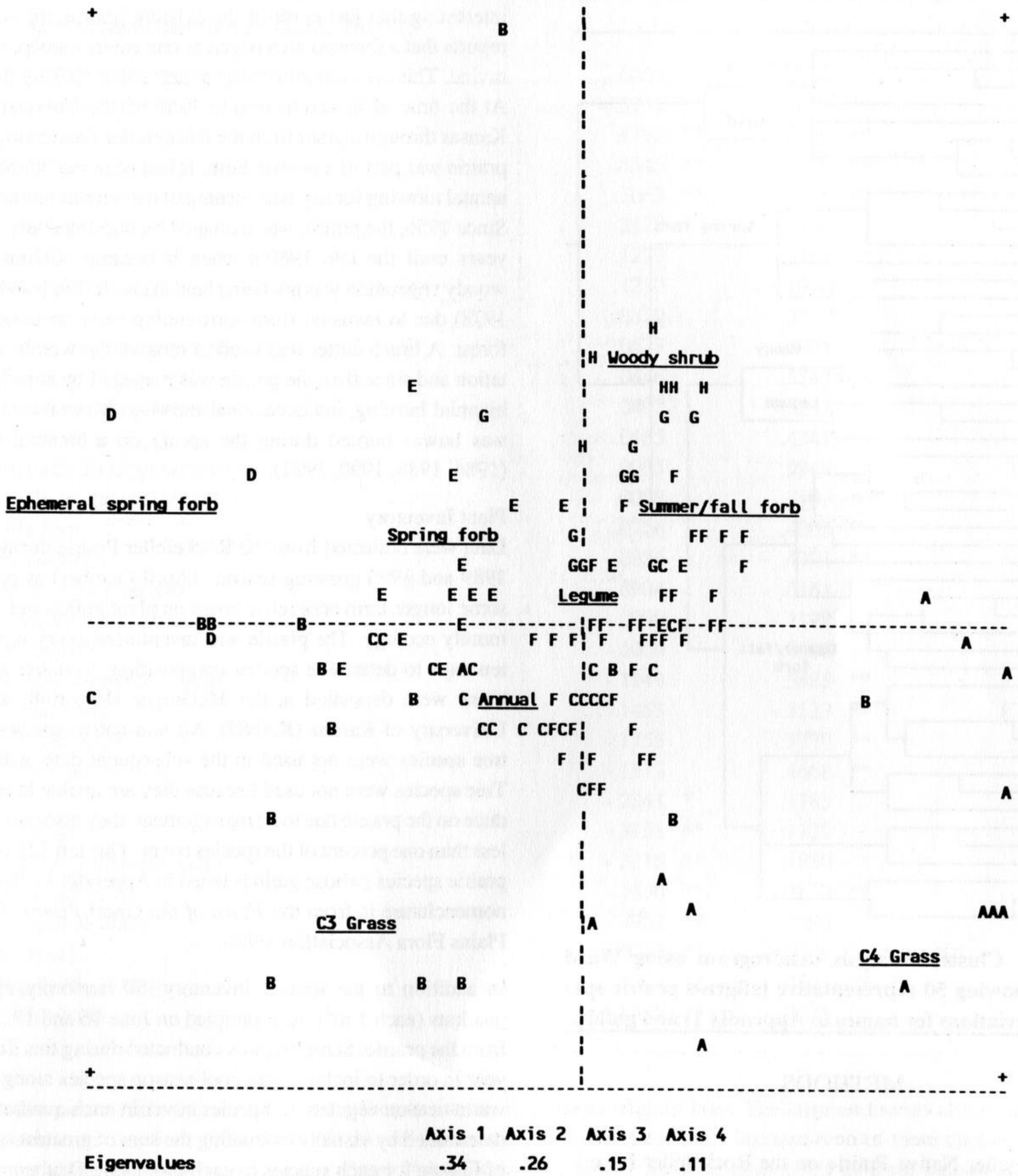


Figure 2. Guild groupings of species on first two axes of detrended correspondence analysis of species positions from 32 morphological and ecological traits of 121 prairie species on the Rockefeller Prairie, and eigenvalues for the first four axes. Letters mark individual species in the following guilds: A=C_4 grass; B=C_3 grass; C=Annual; D=Ephemeral spring forb; E=Spring forb; F=Summer and fall forb; G=Legume; and H=Woody shrub.

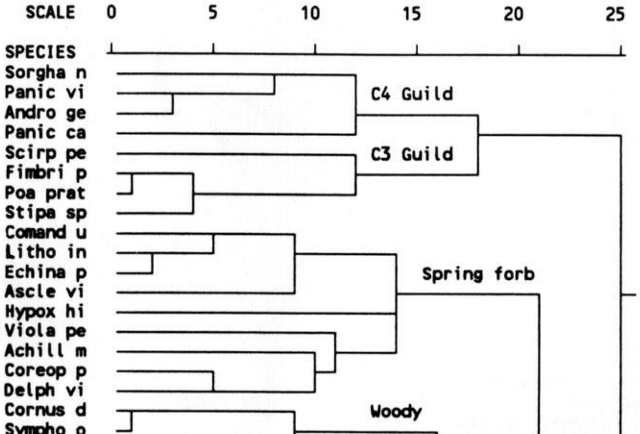


Figure 3. Cluster Analysis dendrogram using Ward method, showing 50 representative tallgrass prairie species (abbreviations for names in Appendix 1) and guilds.

METHODS

Study Site

The Rockefeller Native Prairie on the Rockefeller Experimental Tract of the University of Kansas is known as a highly diverse and floriferous remnant of the original native prairie flora (Fitch and Kettle 1988). It is a 4.6 hectare site, located 12 kilometers north of Lawrence, (Sec. 33, T11S, R20E) in Jefferson County, Kansas. Its soils are Pawnee series and Grundy silty clay loam (both are montmorillonitic, mesic, Aquic Argiudolls).

The U.S. Government land survey for Jefferson County was conducted in 1858, just prior to settlement. It reports that the Rockefeller Native Prairie was indeed in prairie vegetation at that time, as the survey followed the section lines, which included the western and southern sides of the prairie. It is interesting that just north of the existing prairie, the survey reports that a forested area began as one enters a steep, rocky ravine. This area remains today a native oak-hickory forest. At the time of its acquisition in 1956 by the University of Kansas through a grant from the Rockefeller Foundation, the prairie was part of a private farm. It had been maintained by annual mowing for hay and burning of the remaining stubble. Since 1956, the prairie was managed by burning every three years until the late 1960's when it became obvious that woody vegetation was not being held in check (Fitch and Hall 1978) due to invasion from surrounding early-successional forest. A brush cutter was used to remove the woody vegetation and since then the prairie was managed by annual and biennial burning and occasional mowing. More recently, it was buwas burned during the spring on a biennial basis (1986, 1988, 1990, 1992).

Plant Inventory

Data were collected from the Rockefeller Prairie during the 1989 and 1990 growing seasons (April-October) as part of some longer-term ecological work on plant guilds and community ecology. The prairie was inventoried every week to ten days to determine species composition. Voucher specimens were deposited at the McGregor Herbarium at the University of Kansas (KANU). All non-native species and tree species were not used in the subsequent data analysis. Tree species were not used because they are unable to reproduce on the prairie due to its management; they also comprise less than one percent of the species cover. This left 121 native prairie species (whose guild is listed in Appendix 1). Species nomenclature is from the *Flora of the Great Plains* (Great Plains Flora Association 1986).

In addition to the species inventory, 50 randomly placed quadrats (each 1 m^2) were sampled on June 16 and 17, 1989 from the prairie. Sampling was conducted during this time of year in order to include both cool-season species along with warm-season vegetation. Species cover in each quadrat was determined by visually estimating the sum of greatest spread of foliage for each species in each plot using Daubenmire's sampling techniques (Daubenmire 1959).

Guilds of prairie species were previously determined using a multivariate analysis of ecological and morphological traits for species on the Rockefeller Native Prairie and two additional prairies in northeast Kansas (Kindscher 1991). The data below are a subset of the larger data set. They were collected for 32 ecological and morphological traits for each of the 121 native prairie species on the Rockefeller Native Prairie. These 32 traits represent five broad categories: plant habit, leaf characteristics, stem structures, root structures,

Table 1. Variables and correlation coefficients for species positions on the first two axes of a detrended correspondence analysis of 121 prairie species. One-tailed significance: * - 0.01; ** - 0.001.

ECOLOGICAL & MORPHOLOGICAL TRAITS	X1		Y1	
Active growth during warm season	.6069	**	-.0644	
Photosynthetic pathway, C_4	.5732	**	-.4475	**
Flowering, late	.4793	**	-.3656	**
Height, tall	.4345	**	.2926	**
Leaf size, large	.3663	**	.3076	**
Clones, large	.2178	*	.1934	
Seed weight, heavy	.1277		.5504	**
Flowering duration, long	.1210		-.1614	
Woodiness	.0830		.3810	**
Phyllotaxy, opposite or whorled	.0677		.0888	
Zoophilous seed dispersal	.0446		.5247	**
Nitrogen fixation root nodules	.0402		.3291	**
Leaves compound	.0155		.4247	**
Not palatable to large herbivores	.0035		.0948	
Rooting habit, tap or fascicle	.0028		.3401	**
Forb life form	-.0706		.4003	**
Leaves sheathed	-.0836		.4271	**
Leaves hairy or glaucous	-.0904		.0161	
Duration, annual or biennial	-.0990		-.1192	
Leaves divided	-.1009		.0508	
Leaf length/width ratio, large	-.1144		.3885	**
Sod or mat roots	-.1453		-.3123	**
Seed weight, light	-.1755		-.5779	**
Zoophilous pollination	-.1813		.4668	**
Bulbs	-.2241	*	.1185	
Basal rosette	-.3151	**	.1127	
Decumbent or prostrate stem	-.3215	**	.1830	
Leaf size, small	-.3406	**	-.2823	**
Growth period, short	-.3952	**	.0395	
Height, short	-.5203	**	.0009	
Rooting depth, shallow	-.5477	**	-.3121	**
Flowering, early	-.6308	**	.3275	**

and reproduction. Information and data for these traits were collected from the field (Kindscher 1991) and botanical literature (Bare 1979, Steyermark 1981, Great Plains Flora Association 1986), or from the ecological literature (Weaver 1919, 1954, 1968, Weaver and Fitzpatrick 1934, Phillips Petroleum Company 1959, Downton 1975).

The data for these traits are discussed in detail in Kindscher 1991. Traits that reflected the standard or non-specialized types were coded with a 0; those with a specialized trait were coded with a 1. In an effort to make all variables discrete, for four traits (plant height, leaf size, time of flowering, and seed weight) three classes of data were coded by dividing the data into three equal-sized groups (for small or early, medium, and large or late). The large and small classes are coded as specialized traits because each of these classes may confer special adaptive advantages to plant species that have this class trait.

The ordination of species was conducted by using a detrended correspondence analysis using the program CANOCO (ter Braak 1987). Detrended correspondence analyses are useful for ordination of environmental data because they produce results that can more easily be interpreted than other multivariate techniques (Hill and Gauch 1980, Peet et al. 1988). The interpretation of the first two ordination axes was assisted by correlating (using the Pearson product moment) the location of each species in the

Table 2. Canonical discriminant functions including Wilks' lambda and Chi-square and the significance of the functions being the same. Classification results. Abbreviations: Fcn=function; Cum Pct=cummulative percent; DF=degrees of freedom; Sig=significance; ANN=annual; C3=C_3 photosynthestic pathway sedge or grass; C4= C_4 photosynthetic pathway grass; ESP=ephemeral spring forb; FAL=summer or fall forb; SPR=spring forb; LEG=legume; WOO=woody shrub.

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                    Pct of     Cum  Canonical  After  Wilks'
Fcn Eigenvalue Variance   Pct       Corr      Fcn  Lambda  Chisquare     DF  Sig
                                             :  0   .0000   1485.390    140 .0000
  1*    38.6652    47.28   47.28      .9873 :  1   .0000   1095.260    114 .0000
  2*    26.0233    31.82   79.10      .9813 :  2   .0009    745.810     90 .0000
  3*     6.1848     7.56   86.66      .9278 :  3   .0063    536.781     68 .0000
  4*     4.6567     5.69   92.36      .9073 :  4   .0358    353.100     48 .0000
  5*     2.8269     3.46   95.81      .8595 :  5   .1368    210.843     30 .0000
  6*     1.9337     2.36   98.18      .8119 :  6   .4014     96.760     14 .0000
  7*     1.4914     1.82  100.00      .7737 :

  * marks the 7 canonical discriminant functions in the analysis.


Classification Results -

                  No. of   Predicted Group Membership (species per guild)

Actual Group      Cases      1       2       3       4       5       6       7       8
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Group 1  ANN        21      21       0       0       0       0       0       0       0
                        100.0%    0.0%    0.0%    0.0%    0.0%    0.0%    0.0%    0.0%
Group 2  C3         14       0      13       1       0       0       0       0       0
                          0.0%   92.9%    7.1%    0.0%    0.0%    0.0%    0.0%    0.0%
Group 3  C4         14       0       1      13       0       0       0       0       0
                          0.0%    7.1%   92.9%    0.0%    0.0%    0.0%    0.0%    0.0%
Group 4  ESP         4       0       0       0       4       0       0       0       0
                          0.0%    0.0%    0.0%  100.0%    0.0%    0.0%    0.0%    0.0%
Group 5  FAL        34       2       0       0       0      32       0       0       0
                          5.9%    0.0%    0.0%    0.0%   94.1%    0.0%    0.0%    0.0%
Group 6  LEG        10       0       0       0       0       0      10       0       0
                          0.0%    0.0%    0.0%    0.0%    0.0%  100.0%    0.0%    0.0%
Group 7  SPR        18       0       0       0       0       1       0      17       0
                          0.0%    0.0%    0.0%    0.0%    5.6%    0.0%   94.4%    0.0%
Group 8  WOO         6       0       0       0       0       0       0       0       6
                          0.0%    0.0%    0.0%    0.0%    0.0%    0.0%    0.0%  100.0%


Classification Processing Summary
       121 Cases (species) were processed.

Percent of "grouped" cases correctly classified:  95.87%
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detrended correspondence analysis with the 32 ecological and morphological traits (using the raw data matrix). To further corroborate the detrended correspondence analysis ordination, the data set was analyzed through Ward's method of cluster analysis in the program SPSS/PC+ (SPSS 1988). To test the validity of the eight guilds, a discriminant function analysis was performed using Mahalanobis distance as the selection criteria for the data set and using Wilk's lambda and F-tests as test statistics (SPSS, 1988).

Table 3. Total vegetative cover for 50 quadrats for the 20 species with greatest coverage on the Rockefeller Native Prairie. Also included are species of greatest cover for C_3 grass and spring ephemeral guilds; and percent cover/guild, listed in parenthesis adjacent to the species with the greatest cover in each guild. Note that total coverage of all 50 plots for individual species would result in a coverage figure of 50.000. Due to species overlap composite (for all species) total coverage is greater than 50.000.

SPECIES GUILD	(Cover/Guild)	COVER/SPECIES
Andropogon gerardii	C_4 grass (67.5%)	29.020
Andropogon scoparius	C_4 grass	20.320
Silphium laciniatum	Summer/fall forb (16.6%)	5.920
Sporobolus heterolepis	C_4 grass	5.680
Rhus glabra	Woody shrub (7.6%)	5.350
Sorghastrum nutans	C_4 grass	5.030
Amorpha canescens	Legume (5.3%)	2.730
Eryngium yuccifolium	Summer/fall forb	1.880
Solidago rigida	Summer/fall forb	1.685
Helianthus rigidus	Summer/fall forb	1.600
Lespedeza violacea	Legume	1.530
Aster praealtus	Summer/fall forb	1.280
Ceanothus herbaceus	Woody shrub	1.170
Tripsacum dactyloides	C_4 grass	1.020
Euphorbia corollata	Spring forb (1.3%)	0.850
Solidago canadensis	Summer/fall forb	0.680
Solidago missouriensis	Summer/fall forb	0.490
Ambrosia artemisiifolia	Annual (0.8%)	0.380
Baptisia bracteata	Legume	0.350
Apocynum cannabinum	Summer/fall forb	0.305
Dichanthelium oligosanthes	C_3 grass (0.5%)	0.115
Viola pedatifida	Spring ephemeral (0.1%)	0.065
*** Total for above species		87.450
*** Total for 176 Species ***		90.670

DISCUSSION

A total of 176 species was found on the Rockefeller Native Prairie. Of these species, 165 are native; 10 of these occur only along the forest edge, which is being encroached by successional woody species; seven others are tree species that will not reproduce on the prairie due to management (fire or mowing), which reduces them to root sprouts; and 27 were rare or uncommon and data could not be obtained for all 32 traits. The remaining 121 native prairie species were used in the multivariate analysis.

The first axis of the detrended correspondence analysis explained 34% of the variation and the first four axes explained 86% of the variation. The arrangement of species in two-dimensional space shows guild groupings (Figure 1). Eight guilds of prairie species were verified in this analysis: C_4 photosynthetic pathway grasses, C_3 grasses and sedges, annuals and biennials, ephemeral spring forbs, spring forbs, summer/fall forbs, legumes, and woody shrubs (Figure 2). These guilds were previously determined by making logical groupings of the species ordination conducted through the detrended correspondence analysis (Kindscher 1991). Each native species on the Rockefeller Prairie was assigned to a guild (Appendix 1). Some species are listed in two guilds, the primary guild being the one of greatest affinity, determined by the detrended correspondence analysis. Correlations of the 121 species positions in the detrended correspondence analysis with the 32 ecological and morphological traits allows for the interpretation of which traits most highly influence the location of these prairie species and subsequently the groups or guilds of species (Table 1). For the X axis, the following ecological and morphological traits had the most significant positive correlations ($p \leq 0.001$): tall height, active growth during the warm season, large leaf size, C_4 photosynthetic pathway, and late flowering. The most significant negative correlations for the X axis are: decumbent or prostrate stem, short height, short growth period, basal rosette, small leaf size, shallow rooting depth, and early flowering.

For the Y axis, the following ecological and morphological traits had the most significant ($p \leq 0.001$) positive correlations (Table 2): forb life form, tall height, large leaf length/width ratio, large leaf size, compound leaves, sheathed leaves, woodiness, tap or fascicle roots, shallow rooting depth, early flowering, zoophilous pollination, zoophilous seed dispersal, and heavy seed weight. The traits most negatively correlated with the Y axis are: small leaf size, C_4 photosynthetic pathway, sod or mat roots, shallow rooting depth, late flowering, and light seed weight.

The cluster analysis of the data resulted in similar groupings as identified in Figure 3, which added corroborative evidence to the existence of the guilds. The C_3 and C_4 grass guilds were the most clearly defined groups. The summer/fall forb, spring forb, woody shrub, and legume guilds are also distinguishable clusters. Due to the small number of species (four) in the early spring ephemeral forb guild, this group is not clearly distinguishable, nor is the highly variable guild of annuals. It should also be noted that on this prairie, these two guilds only comprised 0.1% and 0.8% respectively of the total vegetative cover sampled.

The discriminant function analysis (Table 2) provides statistical evidence that these eight guilds represent the data set as 95.9% of the prairie species were correctly classified into one of the eight prairie plant guilds. This was confirmed with a 95.0% correct classification for the guilds when this prairie was combined with the original two other high-quality prairies from northeast Kansas (Kindscher, unpublished).

Plant Sampling

The twenty-two species with the highest total coverage ranged from 0.065 m^2 to 29.02 m^2 of the total cover with 50 m^2 being complete cover of all plots (Table 3). Because species overlap, total estimated cover values for all species per plot were greater than 1.00 m^2 (100%), averaging 1.84 m^2 (184%) per plot. Composite plot values of greater than 1.00 m^2 (100%) occurred because almost all plots were dominated by warm season grasses that had a variety of other herbaceous species that overlapped the grass cover. The two species with the greatest total cover were the warm season, C_4 photosynthetic pathway grasses, big bluestem (*Andropogon gerardii*), and little bluestem (*A. scoparius*, synonym = *Schizachyrium scoparium*). The forb with the greatest coverage was compass plant, (*Silphium laciniatum*) (Table 3).

Guilds of Species on the Rockefeller Native Prairie

Using the cover data from quadrats and the entire species list, the eight guilds will be discussed. The traits with significant correlation coefficients will be used to characterized each guild of species. They are discussed in general terms in order that these guild descriptions could be used to classify other prairie species into guilds.

C_4 photosynthetic pathway grasses

This guild (Appendix 1) of 13 species (10.7% of the 121 prairie species in the ordination) dominates the visual appearance of the Rockefeller Native Prairie. The cover data for this prairie provide evidence for the dominance of the C_4 grasses as they compose 67.5% of the total cover. Of particular note in this prairie is the relatively high cover value of prairie dropseed (*Sporobolus heterolepis*) (5.68% of total), and the low cover (only 0.2% of total) of the often dominant switchgrass (*Panicum virgatum*).

Dominance of the C_4 grass guild is widespread (Weaver and Fitzpatrick 1934, Curtis 1959, Ray 1959, Dix and Smeins 1967, Weaver 1968, and Diamond and Smeins 1985). The guild of C_4 grasses essentially forms the matrix of vegetation within which species of other guilds occur. In addition to these ecological and morphological traits, C_4 grasses respond positively to fire and grazing (Hulbert 1969, Peet et al. 1976, and Collins and Wallace 1990).

C_3 photosynthetic pathway grasses and sedges

This guild of 13 species (10.7% of the prairie species ordered) is common to this and other prairies; however, it is not abundant (comprising only 0.5% of the cover of this prairie). The species are known as cool-season grasses, as they flower in the spring, although most have green foliage during the summer (Weaver 1954). The sedges formed a minor component of the cover of this guild.

Annuals

This guild is comprised of 20 opportunistic species (16.5% of the prairie species present) that generally colonize sites of micro-disturbance or survive in bare soil between other species. In a prairie such as this one, with a consistent management history of burning and mowing, annuals make up very little (only 0.8%) of the cover by species. The cover values of annuals generally increase through disturbance (Drew 1947, Launchbaugh 1955, Collins 1987, and Gibson 1989).

Many annual species on the Rockefeller Native Prairie, such as peppergrass (*Lepidium virginicum*) and spotted spurge (*Eupatorium maculata*), are found only along the foot path and in areas of shallowest soil. The difficulty that individual annual plants have in surviving on this prairie (and other high-quality prairies) was exemplified by the inability of the generally highly-productive annual sunflower (*Helianthus annuus*) to set seed during the droughty summer of 1989. During the same time, perennial prairie plants produced viable seeds. It should also be noted that many traits in this guild, such as seed weight, plant height, and seasonality were extremely variable among species, reflecting the diversity of annual plant life forms.

Ephemeral spring forbs

This guild has four species (3.3% of the prairie species ordered) that appear very early in the year, never grow very tall, often have ephemeral foliage, losing their photosynthetic abilities during the summer when the taller warm-season grasses over-top them. Although this guild comprised only 0.1% of the cover, its species were frequently encountered in the quadrats sampled.

Spring forbs

This guild of 17 species (14.0% of the prairie species ordered) is similar to the ephemeral spring forb guild, but differs by appearing a few weeks later in the spring, having slightly taller heights, and they are not ephemeral. These species make up much of the showy wildflower bloom characteristic of tallgrass prairies. The cover values for this guild are less that would be assumed based on observation as they comprise only 1.3% of total. This low value exemplifies how showy species may be over-represented in visually-based inventory work. This guild also includes the federally-protected, Mead's milkweed (*Asclepias meadii*).

Summer/fall forbs

This guild of 36 species (29.6% of the prairie species present) comprises the largest number of species in any guild. These species are generally tall and coarse forbs, that grow along with the warm-season grasses, flowering and setting seed in the summer and fall. Due to the large size of species, this guild comprises 16.6% of the total cover. It also includes the federally-protected, western prairie-fringed orchid (*Habenaria leucophaea*) {synonym = *Platanthera praeclara*}. In addition, this guild contains species that have either wind-dispersal of light seed (*Aster* and *Solidago*) or gravity dispersal of heavier seeds (*Helianthus* and *Silphium*).

Legumes

This guild of 10 species (8.3% of the prairie species ordered) is comprised of a group of variable species that have compound leaves with an odd number of leaflets and apparently have a competitive advantage due to their ability to fix atmospheric nitrogen (Bare 1979). The total cover of this group is 5.3%. Two species in this guild are also part of another guild. Showy partridge pea (*Cassia chamaecrista*) is both a legume and an annual; and leadplant (*Amorpha canescens*) is both a legume and a woody shrub. Both were classified with the legume guild due to their locations in the detrended correspondence analysis.

Woody shrubs

This guild of 6 species (5.0% of the prairie species ordered) is comprised of woody species which have some of their overwintering buds above the ground's surface. These species, which persist in managed prairie remnants, are those that resist the effects of fire and mowing. Pastures are often invaded by trees, but trees do not generally reproduce when clipping (whether by grazing or machinery) is accompanied by fire. This guild represents 7.6% of the total cover. It is perhaps over-represented in cover on the Rockefeller Native Prairie due to the quadrat transects passing through a dense colony of smooth sumac (*Rhus glabra*). The spread of this colony and the invasion of other woody species from the surrounding areas of early-successional forest is of concern to the management of this prairie, and resulted in the frequency of burning or mowing being increased to every other year. The dense stand of sumac also provides habitat for some weedy understory forest species not found elsewhere in the prairie (white snakeroot {*Eupatorium rugosum*} and bittersweet {*Celastrus scandens*}), which are invading from the surrounding forest.

Other species not in prairie guilds

The species not represented in the above guilds include trees, forest edge species, and non-native species. All these species were rarely on the quadrats and had very low total cover values (their combined cover values are only 0.2% of the total). Trees such as box elder (*Acer negundo*) and slippery elm (*Ulmus rubra*) are unable to reproduce on the prairie due to management. It appears that the seed rain of early successional forest species, which surround the Rockefeller Native Prairie, would quickly change the species composition of this prairie if management by fire or mowing would cease. Forest edge species, including the weedy, black snakeroot (*Sanicula gregaria*) and gooseberry (*Ribes missouriense*), do not seem to be able to compete on the prairie and are restricted only to its shady edge or in the dense stand of smooth sumac (*Rhus glabra*). Non-native species, such as tansy mustard (*Descurainia pinnata*) and day flower (*Commelina communis*) are weedy and generally located along the edges and elsewhere in small areas of disturbed soil.

Classification of Tallgrass Prairie

The current methodologies used by ecologists for the classification, and subsequent recommended protection of prairies, such as through state natural heritage programs or state departments of natural resources, are based on species presence (especially designated indicator species) and especially presence of federally listed threatened and endangered species. In some cases, classification of prairies has been based on species coverage in quadrats; however, a considerable amount of time to conduct field work and statistical analysis is necessary for quadrat analysis and therefore it is generally not used by these programs.

Classification of tallgrass prairies, and determination of their quality, could be based on the analysis of guilds. They can be incorporated into survey work and ecological studies at various levels of analysis. At the most simplistic level, prairie species guilds can be used to quickly identify an area as native tallgrass prairie, even by those who do not know the identification of many prairie species. The identification process can be done through the use of guild identifications that follow:

Guild Identifications

C_4 photosynthetic pathway grasses--tall, warm season grasses, with flowers and fruit on stalks greater than three feet tall, flowering time mid-summer through fall; narrow, long leaves, often shades of red and orange in the fall;

C_3 photosynthetic pathway grasses and sedges--shorter (usually less than three feet tall), flowers and fruit (at least the onset) before summer, narrow long leaves, with no special coloration in the fall;

Annuals--No perennial root stock; variety of heights and leaf sizes and shapes; usually very fruitful (with many flowers, often not showy); generally found only in disturbed prairie areas;

Ephemeral spring forbs--very short, start flowering very early in the spring (March, usually), flowers usually showy, foliage dries up before summer;

Spring forbs--short, flowering occurs during the spring, often showy flowers and broad leaves; foliage persists into the summer;

Summer/fall forbs--variety of heights (many tall and coarse), flowering occurs during the summer and fall, and usually with non-linear leaves;

Legumes--usually evident during spring or summer, with odd number of leaflets, and flowers with typical pea-shape (bilaterally symmetrical); nitrogen-fixation root nodules present (but difficult to unearth and find);

Woody shrubs--medium to tall in height (but not trees), stems woody, found throughout the growing season, ability to resprout after fire or mowing.

A high-quality tallgrass prairie will probably have all of the guilds present. In three prairies previously studied, all eight guilds have been found (Kindscher 1991). June is the ideal month for survey work. If the survey work is done after June and before March, it may be difficult for the untrained person to determine if the ephemeral spring forb guild exists. The other seven guilds should be visually present.

Tallgrass prairies are relatively similar in species composition throughout their range (Weaver 1954, 1968). These guilds of species exist on tallgrass prairies in Manitoba, Canada, northern Iowa, eastern Nebraska, eastern Kansas, western Missouri, northern Oklahoma, and north-central Texas (Weaver 1954, 1968, personal observation, 1987-1990). They would also be found on tallgrass prairies outside this range, especially to the east and northeast. Midgrass and shortgrass prairies would be different, but would probably have many similarities in guild associations.

A second use of these guilds would be by those experienced in prairie plant species identification and can include guilds in their analysis. There has been much difficulty in determining which tallgrass prairie species are good indicators of high-quality prairies, that is prairies that are high in biodiversity. Even the suggested indicator species, lead plant (*Amorpha canescens*) and compass plant (*Silphium laciniatum*) (Gould 1941, Weaver 1954, Curtis 1959, Weaver 1968), are often found on non-prairie sites, especially disturbed roadsides and parcels planted to introduced cool-season grasses. Perhaps it would be easier and more informative to list the guilds of a tract of land being surveyed and two conservative or unusual species for each guild, than to use indicator species. The species listed could then give a good indication of the range of species found on the tract. This methodology will also lessen the bias of using showy forb species as the indicator species of a high-quality prairie. The use of guild classification and the listing of the most important species on the tract for each guild can also be useful in endangered species surveys and determinations of their associated species complexes.

A third, and possibly the most important, use of guilds is their incorporation into traditional statistical analysis of vegetative cover. For detailed field work that attempts to determine the actual composition of a tract of land, traditional canopy coverage analysis of plot data can be accompanied by guild analysis. The work conducted in this study of the Rockefeller Native Prairie can serve as a model example of integration of these techniques. By using the guild identifications above, native prairie species in addition to the 121 species listed in this study (Appendix 1) can easily be classified into guilds by plant ecologists who are familiar with the species in question. With the species categorized into guilds, it is then possible to supplement canopy coverage of plots with canopy coverage by guild of plots and then to determine what the coverage of each of these guilds is for a particular tract of land. The percent coverage by the guilds can help interpret the type and quality of the vegetation of a prairie remnant. As an example, on high-quality prairies, the coverage of the annual guild would be expected to be small and lower than on a prairie that has been degraded through over-grazing by livestock, or human disturbance.

Guild groupings can be a useful tool in increasing our understanding of the tallgrass prairie. They simplify the array of species into groups in order that ecosystem processes and functions can more easily be studied. They also can allow for a better understanding and interpretation of the diversity of life forms and life history of tallgrass prairie species. For more rigorous analysis of prairies, traditional statistical techniques for analysis of both species and guild groupings can be used to give a clearer understanding of species composition and community classification of tallgrass prairies.

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Appendix 1. Species (grouped by Family), Authority, Common Name, Abundance Code, Primary Guild, Secondary Guild, Total Cover in 50 m^2 Plots. Frequency Codes: C=Common; F=Frequent; I=Infrequent; E=Edge Only; and R=Rare. Guild codes are: ANN=annual; ESP=ephemeral spring forb; FAL=summer or fall forb; SPR=spring forb; LEG=legume; WOO=woody shrub; C3=C$_3$ photosynthetic pathway grass; and C4=C$_4$ grass. Additional codes for species not included in guild-determining multivariate analysis, but found at the site: INTR=introduced species; TREE=tree species; and EDGE=understory woodland species.

SPECIES	AUTHORITY	COMMON NAME	ABUNDANCE CODE	PRIMARY GUILD	SECOND GUILD	COVER
** FAMILY: Acanthaceae						
Ruellia humilis	Nutt.	Fringeleaf ruellia	I	SPR		0.040
** FAMILY: Aceraceae						
Acer negundo	L.	Box elder	I		TREE	0.000
** FAMILY: Amaranthaceae						
Amaranthus rudis	Sauer	Water hemp	I		ANN	0.000
** FAMILY: Anacardiaceae						
Rhus aromatica	Ait.	Fragrant sumac	E		WOO	0.000
Rhus copallina	L.	Dwarf sumac	I		WOO	0.000
Rhus glabra	L.	Smooth sumac	F	WOO		5.350
Toxicodendron radicans	(L.) O. Ktze.	Poison ivy	I		WOO	0.000
** FAMILY: Apiaceae						
Eryngium yuccifolium	Michx.	Button snakeroot	F	FAL		1.880
Polytaenia nuttallii	DC.	Prairie parsley	I		SPR	0.000
Sanicula gregaria	Bickn.	Black snakeroot	E		EDGE	0.000
** FAMILY: Apocynaceae						
Apocynum cannabinum	L.	Indian hemp dogbane	I	FAL		0.305
** FAMILY: Asclepiadaceae						
Asclepias meadii	Torr.	Mead's milkweed	R	SPR		0.000
Asclepias stenophylla	A.	Narrow-leaved milkweed	R	FAL		0.000
Asclepias syriaca	L.	Common milkweed	I	FAL		0.000
Asclepias tuberosa	L.	Butterfly milkweed	R	SPR		0.205
Asclepias verticillata	L.	Whorled milkweed	R	FAL		0.010
Asclepias viridis	Walt.	Spider milkweed	R	SPR		0.000
** FAMILY: Asteraceae						
Achillea millefolium	L.	Yarrow	I	ESP		0.000
Ambrosia artemisiifolia	L.	Common ragweed	I	ANN		0.380
Ambrosia psilostachya	DC.	Western ragweed	I	FAL		0.000
Ambrosia trifida	L.	Giant ragweed	I	ANN		0.000
Antennaria neglecta	Greene	Field pussy-toes	I	SPR		0.000
Artemisia ludoviciana	Nutt.	White sage	I	FAL		0.000
Aster ericoides	L.	White aster	I	FAL		0.000
Aster oolentangiensis	Ridd.	Azure aster	I	FAL		0.250
Aster pilosus	Willd.	Aster	I	FAL		0.135
Aster praealtus	Poir.	Willowleaf aster	F	FAL		1.280
Bidens polylepis	Blake	Coreopsis begger-ticks	I	ANN		0.010
Cacalia plantaginea	(Raf.) Shinners	Indian plantain	R	FAL		0.000
Cirsium altissimum	(L.) Spreng.	Tall thistle	I	FAL		0.000
Conyza canadensis	(L.) Cronq.	Horseweed	I	ANN		0.005
Coreopsis palmata	Nutt.	Finger coreopsis	I	SPR		0.000
Echinacea pallida	Nutt.	Purple coneflower	I	SPR		0.000
Erigeron strigosus	Muhl.	Fleabane	I	ANN		0.025

Appendix 1, continued.

SPECIES	AUTHORITY	COMMON NAME	ABUNDANCE CODE	PRIMARY GUILD	SECOND GUILD	COVER
Eupatorium altissimum	L.	Tall boneset	I		FAL	0.000
Eupatorium rugosum	Houtt.	White snakeroot	I		EDGE	0.040
Euthamia gymnospermoides	Greene	Viscid euthamia	I	FAL		0.000
Helianthus annuus	L.	Annual sunflower	I	ANN		0.010
Helianthus grosseserratus	Martens	Sawtooth sunflower	I	FAL		0.300
Helianthus hirsutus	Raf.	Hairy sunflower	I	FAL		0.000
Helianthus rigidus	(Cass.)	Stiff sunflower	I	FAL		1.600
Krigia caespitosa	(Raf.) Chambers	Dwarf dandelion	I	ANN		0.000
Kuhnia eupatoriodes	L.	False boneset	I	FAL		0.065
Lactuca ludoviciana	(Nutt.) Ridd.	Wild lettuce	I	SPR		0.000
Lactuca serriola	L.	Prickly lettuce	I		INTR	0.000
Liatris aspera	Michx.	Gay-feather	R	FAL		0.000
Liatris pycnostachya	Michx.	Gay-feather	I	FAL		0.000
Prenanthes aspera	Michx.	Rattlesnake-root	R		FAL	0.000
Ratibida pinnata	(Vent.) Barnh.	Grayhead prairie coneflower	I	FA		0.000
Rudbeckia hirta	L.	Black-eyed susan	I	FAL		0.000
Silphium laciniatum	L.	Compass plant	F	FAL		5.920
Solidago canadensis	L.	Canada goldenrod	I	FAL		0.680
Solidago missourensis	Nutt.	Prairie goldenrod	I	FAL		0.490
Solidago rigida	L.	Stiff goldenrod	F	FAL		1.685
Taraxacum officinale	Weber	Dandelion	E		INTR	0.000
Vernonia baldwinii	Torr.	Ironweed	I	FAL		0.000
** FAMILY: Berberidaceae						
Podophyllum peltatum	L.	May apple	E		EDGE	0.000
** FAMILY: Boraginaceae						
Hackelia virginiana	(L.)I.M. Johnst.	Stickseed	E		EDGE	0.000
Lithospermum canescens	(Michx.) Lehm.	Puccoon	I	SPR		0.000
Lithospermum incisum	Lehm.	Puccoon	I	SPR		0.000
Myosotis verna	Nutt.	Forget-me-not	I	ANN		0.005
** FAMILY: Brassicaceae						
Alliaria petiolata	(Bieb.) Cavara & Grande	Garlic mustard	E		INTR	0.000
Descurainia pinnata	(Walt.) Britt.	Tansy mustard	E		INTR	0.000
Lepidium virginicum	L.	Peppergrass	I	ANN		0.000
Thlaspi arvense	L.	Field pennycress	E		INTR	0.000
** FAMILY: Caesalpiniaceae						
Cassia chamaecrista	L.	Showy partridge pea	I	LEG	ANN	0.010
** FAMILY: Campanulaceae						
Triodanis perfoliata	(L). Nieuw.	Venus' looking glass	I	ANN		0.035
** FAMILY: Caprifoliaceae						
Symphoricarpos orbiculatus	Moench	Buckbrush	I	WOO		0.005
Triosteum perfoliatum	L.	Horse gentian	I		EDGE	0.000

Appendix 1, continued.

SPECIES	AUTHORITY	COMMON NAME	ABUNDANCE CODE	PRIMARY GUILD	SECOND GUILD	COVER
** FAMILY: Caryophyllaceae						
Silene antirrhina	L.	Sleepy catchfly	I	ANN		0.025
** FAMILY: Celastraceae						
Celastrus scandens	L.	Bittersweet	I		TREE	0.000
** FAMILY: Chenopodiaceae						
Chenopodium berlandieri	Moq.	Lamb's quarters	I	ANN		0.000
** FAMILY: Clusiaceae						
Hypericum perforatum	L.	Common St. John's-wort	I		INTR	0.000
** FAMILY: Commelinaceae						
Commelina communis	L.	Dayflower	I		INTR	0.000
Tradescantia ohiensis	Raf.	Spiderwort	R	SPR		0.000
** FAMILY: Cornaceae						
Cornus drummondii	C.	Rough-leaved dogwood	I	WOO		0.215
** FAMILY: Cuscutaceae						
Cuscuta glomerata	Choisy.	Dodder	I		EDGE	0.000
** FAMILY: Cyperaceae						
Carex brevior	(Dew.) Mack.	Sedge	I	C3		0.115
Carex davisii	Schwein. & Torr.	Sedge	I		C3	0.000
Carex meadii	Dew.	Sedge	I	C3		0.110
Fimbristylis puberula	(Michx.) Vahl.	Sedge	I	C3		0.000
Scirpus pendulus	Muhl.	Bulrush	R	C3		0.000
Scleria triglomerata	Michx.	Nut rush	I	C3		0.010
** FAMILY: Euphorbiaceae						
Acalypha virginica	L.	Three-seeded mercury	I	ANN		0.210
Croton capitatus	Michx.	Woolly croton	I	ANN		0.005
Euphorbia corollata	L.	Flowering spurge	I	SPR		0.850
Euphorbia cyathophora	Murray	Fire-on-the-mountain	I		ANN	0.000
Euphorbia dentata	Michx.	Toothed spurge	I	ANN		0.000
Euphorbia maculata	L.	Spotted spurge	I	ANN	C4	0.000
Euphorbia nutans	Lag.	Eyebane	E		ANN	0.000
** FAMILY: Fabaceae						
Amorpha canescens	Pursh	Leadplant	I	LEG		2.730
Baptisia bracteata	Muhl ex Ell.	Yellow wild indigo	I	LEG		0.350
Baptisia lactea	(Raf.) Thieret.	White wild indigo	I	LEG		0.000
Dalea candida	Michx.	White prairie clover	I	LEG		0.000
Dalea purpurea	Vent.	Purple prairie clover	I	LEG		0.000
Desmodium glutinosum	(Muhl. ex Willd.) Wood	Large-flowered tickclover	I		EDGE	0.000
Desmodium illinoense	A. Gray	Illinois tickclover	I	LEG		0.020
Desmodium sessilifolium	(Torr.) T. & G.	Sessile-leaved tickclover	C	LEG		0.030
Lespedeza capitata	Michx.	Round-head lespedeza	I	LEG		0.115
Lespedeza stipulacea	Maxim.	Korean lespedeza	I		INTR	0.000

Appendix 1, continued.

SPECIES	AUTHORITY	COMMON NAME	ABUNDANCE CODE	PRIMARY GUILD	SECOND GUILD	COVER
Lespedeza violacea	(L.) Pers.	Prairie lespedeza	I	LEG		1.530
Psoralea esculenta	Pursh	Prairie turnip	R		LEG	0.000
Psoralea tenuiflora	Pursh	Wild alfalfa	I	LEG		0.000
Strophostyles leiosperma	(T. and G.) Piper	Slick-seed bean	I		ANN	0.005
** FAMILY: Fagaceae						
Quercus muehlenbergii	Engelm.	Chinkapin oak	I		TREE	0.000
Quercus velutina	Lam.	Black oak	E		TREE	0.000
** FAMILY: Fumariaceae						
Gentiana puberulenta	Pringle	Downy gentian	R	FAL		0.060
** FAMILY: Geraniaceae						
Geranium carolinianum	L.	Cranesbill	I	ANN		0.010
** FAMILY: Grossulariaceae						
Ribes missouriense	Nutt.	Gooseberry	E		EDGE	0.000
** FAMILY: Juglandaceae						
Juglans nigra	L.	Black walnut	I		TREE	0.000
** FAMILY: Juncaceae						
Juncus interior	Wieg.	Inland rush	I	C3		0.000
** FAMILY: Lamiaceae						
Monarda fistulosa	L.	Wild bergamont	I	FAL		0.000
Pycnanthemum tenuifolium	Schrad.	Slender-mountian mint	I	FAL		0.175
Salvia azurea	Lam.	Pitcher sage	I	FAL		0.205
Teucrium canadense	L.	American germander	I	FAL		0.000
** FAMILY: Liliaceae						
Allium vineale	L.	Wild onion	E		INTR	0.000
Hypoxis hirsuta	(L.) Cov.	Yellow star grass	F	ESP		0.000
Sisyrinchium campestre	Bickn.	White-eyed grass	I	ESP		0.000
** FAMILY: Linaceae						
Linum sulcatum	Ridd.	Grooved flax	I	ANN		0.005
** FAMILY: Moraceae						
Morus alba	L.	Mulberry	I		TREE	0.030
** FAMILY: Nyctaginaceae						
Mirabilis albida	(Walt.) Heimerl.	White four o'clock	I	SPR		0.000
Mirabilis nyctaginea	(Michx.) MacM.	Wild four o'clock	I	SPR		0.000
** FAMILY: Oleaceae						
Fraxinus americana	L.	White ash	I		TREE	0.000
** FAMILY: Onagraceae						
Gaura longiflora	Spach	Large-flowered gaura	I	FAL		0.035
Oenothera villosa	Thunb.	Common evening primrose	I		FAL	0.000
** FAMILY: Orchidaceae						
Habenaria leucophaea	(Nutt.) A Gray	Prairie fringed orchid	R		FAL	0.000

Appendix 1, continued.

SPECIES	AUTHORITY	COMMON NAME	ABUNDANCE CODE	PRIMARY GUILD	SECOND GUILD	COVER
** FAMILY: Oxalidaceae						
Oxalis dillenii	Jacq.	Gray-green wood sorrel	I	SPR		0.100
Oxalis violacea	L.	Violet wood sorrel	I		SPR	0.000
** FAMILY: Plantaginaceae						
Plantago virginica	L.	Pale-seeded plantain	I		INTR	0.000
** FAMILY: Poaceae						
Agrostis hyemalis	(Walt.) B.S.P.	Ticklegrass	I	C3		0.000
Andropogon gerardii	Vitman	Big bluestem	C	C4		29.020
Andropogon scoparius	Michx.	Little bluestem	C	C4		20.320
Bouteloua curtipendula	(Michx.) Torr.	Sideoats grama	C	C4		0.000
Bromus inermis	Leyss.	Smooth brome	I		INTR	0.000
Dichanthelium acuminatum	(Sw.) Gould & Clark	Panic grass	I	C3		0.000
Dichanthelium oligosanthes	(Schult.) Gould	Scribner dichanthelium	I	C3		0.115
Elymus canadensis	L.	Canada wild rye	I	C3		0.030
Elymus virginicus	L.	Virginia wild rye	I	C3		0.000
Eragrostis spectabilis	(Pursh) Steud.	Purple lovegrass	I	C4		0.000
Koeleria pyramidata	(Lam.) Beauv.	June grass	I	C3		0.000
Muhlenbergia frondosa	(Poir.) Fern.	Wirestem muhly	I		C4	0.000
Muhlenbergia racemosa	(Michx.) B.S.P.	Marsh muhly	R	C4		0.000
Panicum capillare	L.	Common witchgrass	I	C4		0.000
Panicum virgatum	L.	Switchgrass	C	C4		0.160
Poa compressa	L.	Canada bluegrass	I		INTR	0.000
Poa pratensis	L.	Kentucky bluegrass	I	C3		0.090
Sorghastrum nutans	(L.)	Nash Indian grass	C	C4		5.030
Sporobolus asper	Torr.	Rough dropseed	F	C4		0.000
Sporobolus heterolepis	Gray	Prairie dropseed	F	C4		5.680
Stipa spartea	Trin.	Porcupine grass	I	C3		0.010
Tridens flavus	(L). Hitchc.	Redtop	I	C3		0.005
Tripsacum dactyloides	L.	Eastern gammagrass	I	C4		1.020
** FAMILY: Polemoniaceae						
Phlox pilosa	L.	Prairie phlox	I	SPR		0.005
** FAMILY: Polygalaceae						
Polygala verticillata	L.	Whorled milkwort	I		ANN	0.000
** FAMILY: Ranunculaceae						
Anemone virginiana	L.	Tall anemone	E		EDGE	0.000
Delphinium virescens	Nutt.	Prairie larkspur	I	SPR		0.000
** FAMILY: Rhamnaceae						
Ceanothus herbaceous	Raf.	New Jersey tea	I	WOO		1.170
** FAMILY: Rosaceae						
Fragaria virginiana	Duchn.	Wild strawberry	I	UNCL		0.000

Appendix 1, continued.

SPECIES	AUTHORITY	COMMON NAME	ABUNDANCE CODE	PRIMARY GUILD	SECOND GUILD	COVER
Geum canadense	Jacq.	White avens	E		EDGE	0.000
Rosa arkansana	Porter	Prairie wild rose	I	WOO		0.070
Rubus flagellaris	L.	Northern dewberry	I		WOO	0.000
Rubus ostryifolius	Rydb.	High-bush blackberry	I	WOO		0.085
** FAMILY: Rubiaceae						
Galium circaezans	T. & G.	Shining bedstraw	E		EDGE	0.060
Hedyotis crassifolia	Raf.	Small bluets	I	ANN		0.000
** FAMILY: Santalaceae						
Comandra umbellata	(L.) Nutt.	Bastard toadflax	I	SPR		0.000
** FAMILY: Scrophulariaceae						
Veronicastrum virginicum	(L.) Farw.	Culver's root	R	FAL		0.000
** FAMILY: Solanaceae						
Physalis pumila	Nutt.	Prairie ground cherry	I	FAL		0.005
Solanum carolinense	L.	Carolina horse nettle	I	FAL		0.005
** FAMILY: Ulmaceae						
Ulmus rubra	Muhl.	Slippery elm	I		TREE	0.065
** FAMILY: Verbenaceae						
Verbena canadensis	(L.) Britt.	Rose vervain	E		SPR	0.000
Verbena hastata	L.	Blue vervain	E		FAL	0.000
Verbena urticifolia	L.	Nettle-leaved vervain	I		FAL	0.000
** FAMILY: Violaceae						
Viola pedatifida	G. Don	Prairie violet	F	ESP		0.065
** FAMILY: Vitaceae						
Vitis riparia	Michx.	River-bank grape	I		WOO	0.000

FIVE YEARS OF FOLLOWING THE WESTERN PRAIRIE FRINGED ORCHID (*PLATANTHERA PRAECLARA*) ON THE SHEYENNE NATIONAL GRASSLAND, NORTH DAKOTA.

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Abstract. The western prairie fringed orchid (*Platanthera praeclara*) is a federally listed threatened plant species in the United States that is now restricted to isolated tallgrass prairie tracts. In 1987, 160 orchids were permanently marked on 5 sites subjected to a variety of burning and grazing regimes on the Sheyenne National Grassland, in southeastern North Dakota. The number of orchids displaying aboveground growth declined each year from 1988 through 1991. By 1991, only 11% of the original plants were visible; the remainder were assumed to be dormant or dead. Recruitment data collected beginning in 1990 indicated that new orchids were present in the swales in spite of droughty conditions. There were no consistent trends in orchid numbers or densities among sites. Vegetative composition in the swales was dominated by Kentucky bluegrass (*Poa pratensis*) and the invasion of these sandy soils by a noxious weed, leafy spurge (*Euphorbia esula*). Future management efforts will likely focus on the task of reducing leafy spurge without harming the orchid. Until these efforts are successful, concern about the effect of burning and grazing on orchid populations diminishes in importance.

INTRODUCTION

The western prairie fringed orchid (*Platanthera praeclara*) is a federally listed threatened plant species in the United States (U.S. Fish and Wildlife Service 1989). Once distributed throughout much of the tallgrass prairie west of the Mississippi River in the central United States and southern Canada, its current populations are restricted to isolated prairie tracts. The three largest known populations of the western prairie fringed orchid occur in Minnesota and North Dakota in the United States (Sheviak and Bowles 1986) and in southern Manitoba in Canada (Catling and Brownell 1987).

The prairie fringed orchid is a perennial, herbaceous plant arising from a fusiform tuber. Inflorescences are large and showy, with up to 20 or more cream-colored flowers arranged on a spike; plants may reach up to 75 cm in height (Sheviak and Bowles 1986). The western prairie fringed orchid usually occurs in mesic swales or draws in tallgrass prairie. Soils are generally Mollisols. Associated plant species include big and little bluestem (*Andropogon gerardii* and *A. scoparius*), several species of sedges (*Carex* spp.), switchgrass (*Panicum virgatum*), and prairie sandreed (*Calamovilfa longifolia*) (Bowles and Duxbury 1986).

Historically, the tallgrass prairie evolved with periodic fires and bison grazing. Current management activities in orchid habitat include prescribed burning and cattle grazing. On the Sheyenne National Grassland, in addition to burning and cattle grazing, some swales where orchids occur are mowed to enhance cattle use of the vegetation. This research was initiated to provide preliminary data on the life history and habitat of the western prairie fringed orchid in a variety of pastures on the Sheyenne National Grassland.

Study Area

The study was conducted in the Sheyenne National Grassland, in southeastern North Dakota. The National Grassland encompasses approximately 27,244 ha, and is managed by the United States Forest Service. Between 1984-1985, approximately 2,000 western prairie fringed orchids were observed on the National Grassland (Bowles and Duxbury 1986). The plants occur both as isolated individuals and as indistinct subpopulations in lowland depressions. A layer of nearly impervious lake sediments is responsible for the relatively high water table in the swales.

Plant species characteristic of the tallgrass prairie, including big bluestem and little bluestem, occur throughout the study area. Woolly sedge (*Carex lanuginosa*), baltic rush (*Juncus balticus*) and northern reed grass (*Calamagrostis inexpansa*) are common in lowland depressions (Manske 1980). Mixed-grass prairie species such as blue grama (*Bouteloua gracilis*), needle-and-thread grass (*Stipa comata*), sun sedge (*C. heliophila*), and prairie sandreed grow on uplands.

The Sheyenne National Grassland receives an average precipitation of 49.7 cm, 80% of which occurs between April and September (U.S. Dept. Commerce 1973). Precipitation on the study area was above average in 1986, below average in 1987, 1989, and 1990, and slightly above average in 1988 and 1991 (Fig. 1). Sediments deposited in glacial Lake Agassiz constitute the largest portion of the parent materials in the area. Mollisols are the most prevalent soils; Entisols occur in some swales (U.S. Soil Conservation Service 1975).

METHODS

In 1987, 16 belt transects were established on 5 separate study sites in areas of orchid concentrations (Bjugstad and

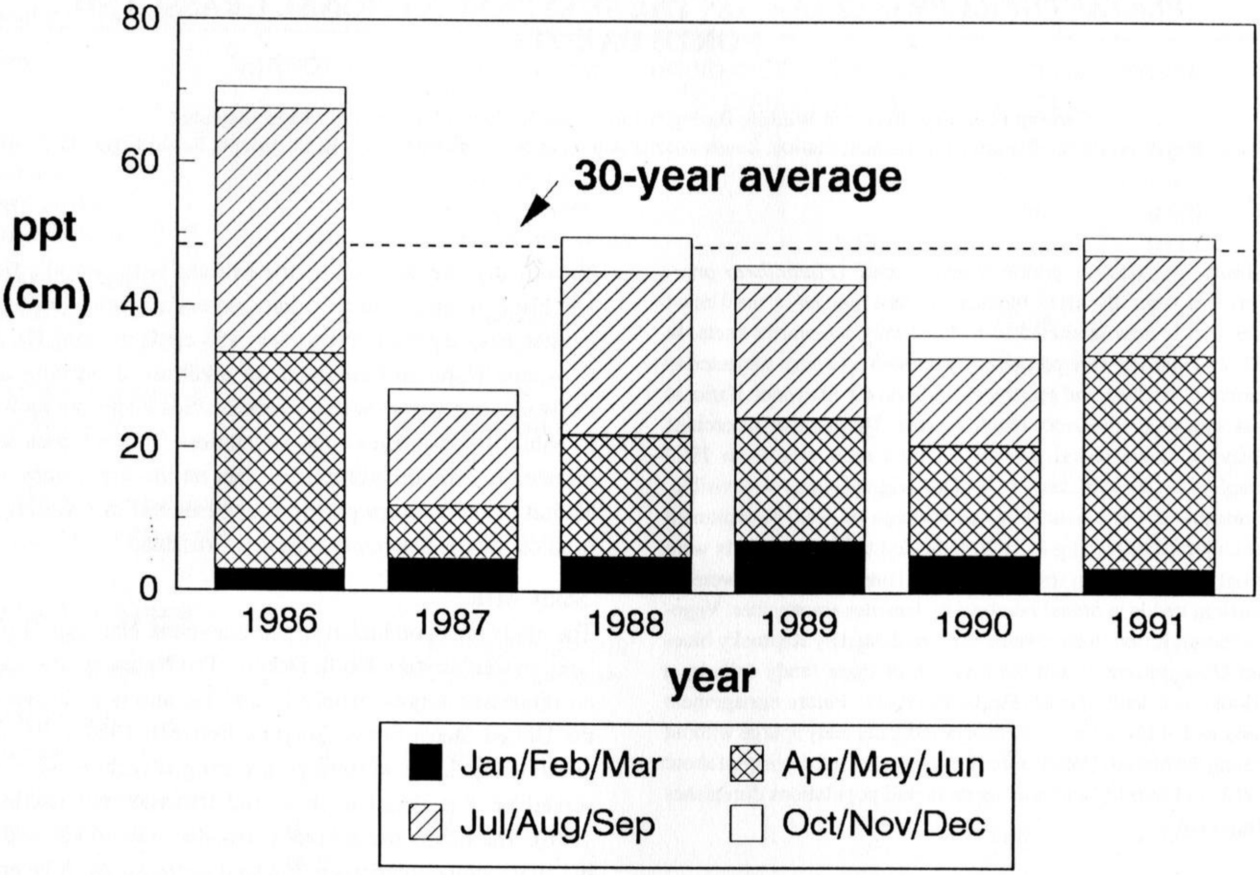

Figure 1. Annual precipitation 1986-1991, showing seasonal distribution, and 30-year average annual precipitation for McLeod, North Dakota, 8 km south of the Sheyenne National Grassland.

Fortune 1989). The 5 study sites included: 1) Olerude; 2) A-Annex; 3) Railroad; 4) Penberthy exclosure; and 5) Penberthy. These sites occur in a core area of the orchid metapopulation on the Sheyenne National Grassland (Fig. 2). Olerude is part of a four-pasture allotment that is grazed by cattle two times during the growing season; some of the swales are mowed. A-Annex is grazed by cattle throughout the growing season. Transects on the Railroad site are not grazed. Both the Penberthy sites were prescribed burned in the spring of 1989; the exclosure transects are not grazed, and the other Penberthy transects are part of a three-pasture allotment that are grazed twice by cattle during the growing season. The belt transects were 30 to 80 m long and 10 m wide. Locations of 10 orchids on each transect were permanently marked in 1987 with plastic-coated steel pins 5 dm from the plant. The 160 orchids were resurveyed each year during flowering (last week in June through the middle of July) from 1988 through 1991. Beginning in 1990, new orchids were marked in addition to the ten orchids originally marked on each transect in 1987.

Plant canopy cover was estimated in 1991 following Daubenmire (1959) in 20- by 50-cm quadrats on each site by 6 cover classes (1 =<5 %, 2 = 6 - 25%, 3 = 26-50%, 4 = 51 - 75%, 5 = 76 - 95%, and 6 = 96 - 100%). A total of 30 to 50 quadrats were examined along the center line of each belt transect. Variables estimated included total plant canopy cover, litter, bare ground, total shrub cover, forb cover, grass cover, and cover by individual plant species.

Soil chemical analyses were conducted in 1988. One soil sample was taken within 15 cm of each permanently-marked orchid to a depth of approximately 20 cm. The 10 samples on each swale were composited into 5 samples. Analyses included particle size distribution (Day 1965), percentage organic matter (Prince 1955), pH (McLean 1982), and calcium (Lanyon and Heald 1982).

Statistical Analyses

Differences in numbers of marked orchids among sites over the five years and in total orchid densities among sites in 1990 and 1991 were analyzed by repeated measures analysis of variance (Norusis 1990). Normality was tested by plotting residuals, and homogeneity of variances was tested using Mauchly's test of sphericity; variances were homogeneous (P >0.1).

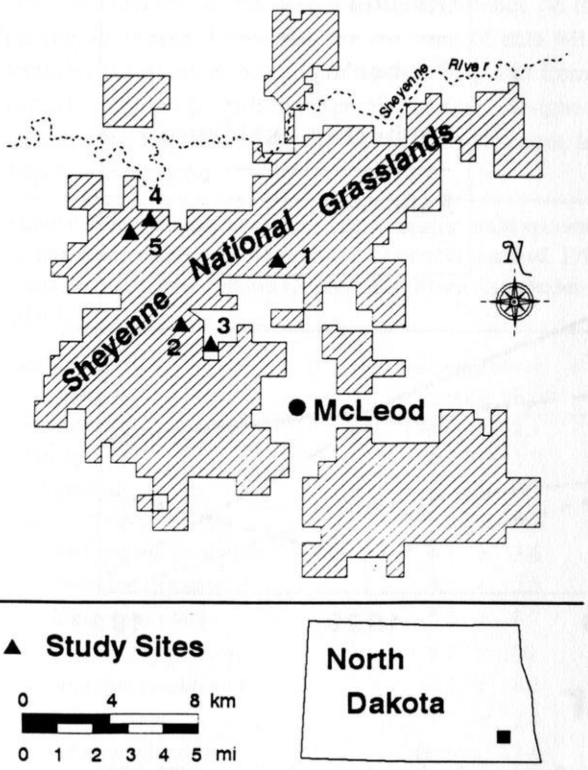

Figure 2. Map of the study area on the Sheyenne National Grassland, in southeastern North Dakota, showing the five study sites: 1) Olerude, 2) A-Annex, 3) Railroad, 4) Penberthy exclosure, and 5) Penberthy.

RESULTS

The number of orchids originally marked in 1987 that reappeared in subsequent years declined significantly (F = 149.14, df = 4, P = 0.0001). By 1991, only 18 of the original plants were observed (Fig. 3). On seven of the transects, none of the original orchids reappeared in 1991. However, the number of orchids reappearing each year did not differ (P = 0.27) among sites, and the significant (P = 0.01) site X year interaction indicated that none of the sites had consistently higher or lower numbers of marked orchids compared to other sites. For example, in 1988, 75% of the marked orchids were relocated on A-Annex; on the Railroad site 65% were observed (Fig. 2). Yet, in 1990, only 5% of the original orchids were observed on A-Annex and Railroad sites, compared to 27% and 25% that were observed on the Penberthy exclosure and on Olerude site, respectively.

The data collected on new orchids beginning in 1990 indicated that most transects had at least one orchid. Up to nine new orchids per transect were observed in 1990; up to 14 new orchids were observed on one transect in 1991. Average orchid density on the 16 transects was 1.1 and 1.2 plants/100m^2 in 1990 and 1992, respectively. The highest density observed in 1990 was 2.4 plants/100m^2; in 1991, the maximum density was 4.0 plants/100m^2. Densities differed (P = 0.02) among sites over the two years, but the significant (P = 0.003) treatment by year interaction indicated that orchid densities were not consistently higher or lower on one site relative to the others during the two years (Table 1).

Total plant canopy cover averaged 96% on the 16 transects; litter cover averaged 96%, and bare ground averaged 1% (Table 2). Total graminoid cover averaged 70%, total forb cover 36%, and total shrub cover 16%. Kentucky bluegrass (*Poa pratensis*) was the dominant species on the 16 transects, followed by a variety of sedges, of which woolly sedge was the most common. Other common graminoids in the swales included baltic rush, switchgrass, northern reedgrass, and Wilcox dichanthelium (*Dicanthelium wilcoxinum*). Strawberry (*Fragaria virginiana*), leafy spurge (*Euphorbia esula*), and Canada anemone (*Anemone canadensis*) were dominant forbs, followed by Canada goldenrod (*Solidago canadensis*) and other species of *Solidago* and perennial ragweed (*Ambrosia psilostachya*). Willows (including *Salix exigua* and *S. bebbiana*) were the most prevalent shrub species.

The majority (59%) of the soils on the 16 swales were sandy loams; 29% of the surface soils were loamy sands and 12% were sandy clay loams. Sand content on the sixteen swales averaged 76.8% (± 5.5 SD), and ranged from 62 - 86%. Silt content averaged 8.6% (± 2.2 SD), and ranged from 3 to 15%. Clay content averaged 14.6% (± 3.9 SD); the range in clay content was 9 - 14%. Organic matter averaged 3.8% and ranged from 0.9 to 5.8%. Soil pH averaged 7.9 (± 0.4 SD), with a range from 6.5 to 8.4. Calcium content averaged 3385.6 ppm (± 768.2 SD) and ranged from 1818 to 4545 ppm.

DISCUSSION

The dramatic decline in the number of original marked orchids since 1987 might be due to dormancy or death. Many species of temperate orchids are characterized by irregularly-spaced periods of dormancy (e.g., Hutchings 1989). The prairie fringed orchids (*Platanthera* spp.) are reported to be long-lived perennial plants, and other researchers have noted episodic aboveground growth followed by years when orchids seem to have disappeared, and have speculated that the plants are in a stage of dormancy induced by drought. In Illinois, Bowles et al. (1992) observed 100 flowering eastern prairie fringed orchids (*P. leucophaea*); the 1988 drought reduced the number of flowering plants to almost none for two years. Lower than average precipitation on our study area

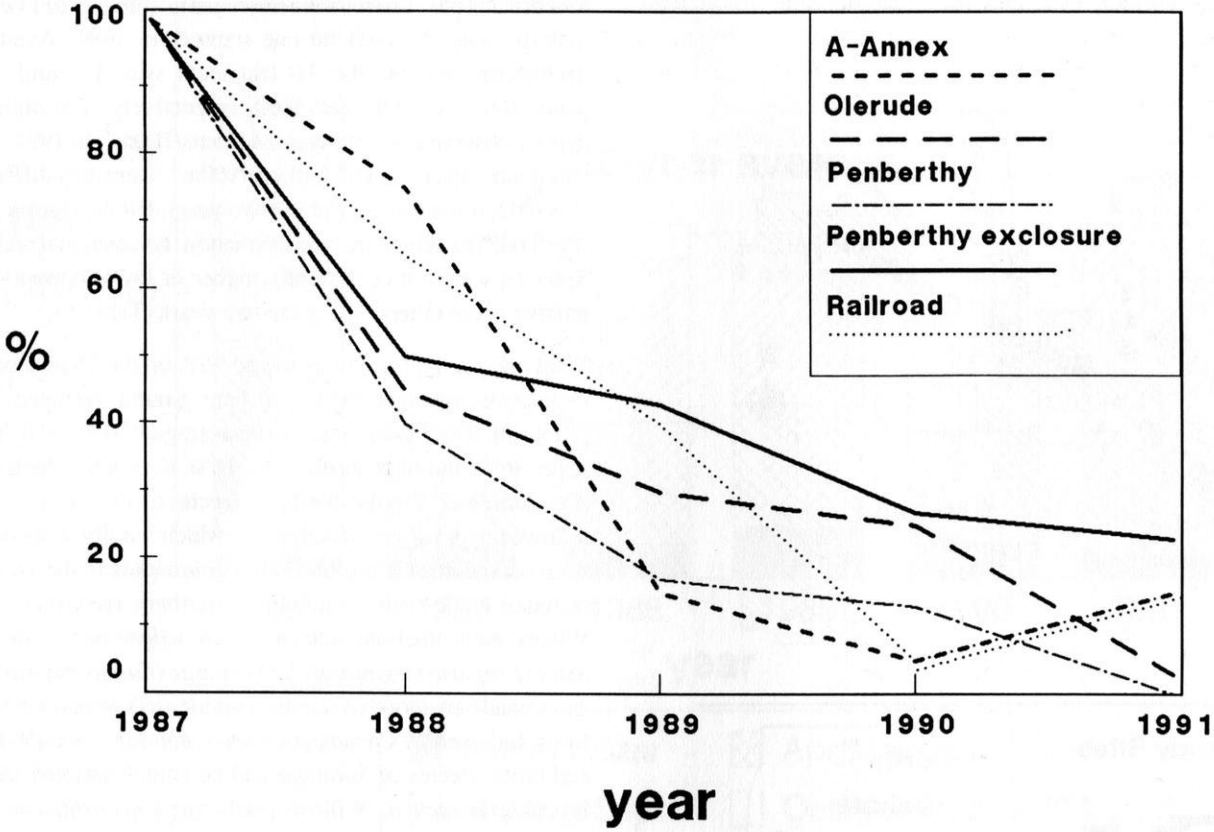

Figure 3. Percentages of permanently marked orchids observed on five burning/grazing regimes in 1987-1991, on the Sheyenne National Grassland, North Dakota.

for three of five years since this study began may have induced dormancy of many orchids.

It is possible that the marked orchids have died. For many orchid species, a dormancy period of 3 to 4 years is the upper limit, beyond which the probability of survival is significantly reduced (Falb and Leopold 1993). However, the presence of other new orchids on the Sheyenne National Grassland is indicative that recruitment is occuring on these sites. Whether the original plants will again reappear remains to be seen. Numbers of eastern prairie fringed orchids were higher in lowlands and in years of high rainfall in Illinois (Bowles et al. 1992). Until the Sheyenne population is observed in high precipitation years, conclusions about the longevity of this orchid are purely speculative.

The absence of any clear trends among sites in numbers of original marked orchids reappearing or in orchid densities should not be interpreted as unequivocal evidence that the orchids are not responding to the various management practices. Rather, it is likely that highly variable orchid densities and droughty conditions are masking effects of management

Table 1. Average ($\bar{x} \pm SE$) orchid density (no./100m^2) per swale on five sites on the Sheyenne National Grassland, 1990-1991.

Site	1990	1991
Olerude	1.00 ± 0.10	0.30 ± 0.13
A-Annex	1.24 ± 0.36	3.07 ± 0.39
Railroad	0.48 ± 0.19	1.35 ± 0.81
Penberthy exclosure	1.53 ± 0.51	1.00 ± 0.30
Penberthy	1.07 ± 0.45	0.13 ± 0.12
Average	1.11 ± 0.16	1.22 ± 0.33

regimes. Further, variations in degree of cattle use of the swales, site quality, depth to water table, soils, and original orchid densities before management was applied are variables to consider in the design of future studies on these orchids. It is very likely that several years of data will be required to sort out effects of management regimes from the behavior of this orchid; and specific studies, designed to measure the impacts of clearly defined management techniques, are required.

Table 2. Plant canopy cover (x ± SE) of major plant species on five study sites on the Sheyenne National Grassland, 1991. Plant nomenclature follows Great Plains Flora Association (1986).

Category Species	Average cover (x ± SE)
Total cover	96.4 ± 1.1
Litter cover	96.2 ± 1.3
Bare ground	0.5 ± 0.7
Total forb cover	35.8 ± 13.7
Ambrosia psilostachya	4.1 ± 3.6
Anemone canadensis	4.9 ± 5.5
Euphorbia esula	5.2 ± 8.7
Fragaria virginiana	6.1 ± 9.0
Solidago canadensis	4.5 ± 4.3
Solidago spp.	1.9 ± 2.4
Total graminoid cover	69.8 ± 17.4
Calamagrostis stricta	6.6 ± 7.5
Carex spp.[1]	14.2 ± 11.1
Dicanthelium wilcoxianum	5.3 ± 7.5
Juncus balticus	12.6 ± 9.7
Panicum virgatum	9.7 ± 8.4
Poa pratensis	27.6 ± 27.3
Spartina pectinata	3.6 ± 5.4
Total shrub cover	16.5 ± 13.4
Salix spp.[2]	12.7 ± 11.5

[1] Includes *Carex lanuginosa*, *C. granularis*, and *C. brevior*

[2] Includes *Salix exigua* and *S. bebbiana*

Plant composition on the 16 swales was quite variable and reflected the problem of introduced species and noxious weeds. Species previously reported to be dominant in these swales, such as northern reedgrass, baltic rush, and woolly sedge (Manske 1980) were less common than Kentucky bluegrass. The domination by Kentucky bluegrass in several swales is a reflection of this species' ability to invade native grasslands; this ability may be further enhanced by cattle grazing and/or mowing (Daubenmire 1978). Swales have also been impacted by the invasion of leafy spurge, a noxious weed. The presence of spurge on all sites except Penberthy indicates the severity of this problem, and highlights the challenge of combatting noxious weeds in areas where rare plants occur.

Current efforts to control leafy spurge on the Sheyenne National Grassland include spraying herbicides (usually a mixture of picloram and 2,4-D), biological control, and goats. Three species of flea beetles (*Aphthona nigriscutis*, *A. cyparissiae*, and *A. flava*) have been released in the area. Adult flea beetles consume spurge leaves and bracts; the larvae feed on roots (Rees and Spencer 1991). Angora goats have also been introduced on the Sheyenne National Grassland on pastures not included in this study. When used with herders, they show some promise for reducing the spread of leafy spurge. Currently, swales supporting orchid populations are avoided in spraying programs, and goats are either not allowed in orchid-supporting swales during the growing season, or the orchids are covered with wire cages to protect them from goat herbivory.

The sandy, alkaline soils that supported orchid populations on the Sheyenne National Grassland differed from those previously reported for other regions. Soil pH in Iowa, Kansas, and Oklahoma were generally acidic (ph 5.4 to 6.4); pH values in Nebraska, North Dakota and Minnesota ranged from 7.4 to 7.5 (Bowles and Duxbury 1986). Soil pH on the Sheyenne study site averaged 7.9, but ranged from 6.5 to 8.4. Calcium content of these soils (1818 - 4545 ppm) tended to be on the lower end of the values previously reported (1730 - 6456 ppm) (Bowles and Duxbury 1986). Organic matter percentages (<1 - 5.8%) were also lower on all sites than those previously reported (6.1 to 23%).

CONCLUSION

It is impossible at this time to draw any conclusions on the effects of various management regimes on orchid populations on the Sheyenne National Grassland. Whether marked orchids will reappear following above normal precipitation remains to be seen. However, the fairly consistent recruitment in 1990 and 1991 is encouraging evidence that the orchid persists. It is likely that a combination of the sporadic growth behavior of the orchid and drought is masking the effects of grazing and burning. What is obvious at this point is the problem of leafy spurge invasion on the National Grassland. In spite of efforts to subdue this noxious weed, it continues to expand in these sandy soils. Future management efforts will likely focus on the task of reducing leafy spurge without harming the orchid. Until these efforts are successful, concern about the effect of burning and grazing on orchid populations diminishes in importance.

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THE SEDGE (*CAREX*) FLORA OF OHIO FENS

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Abstract. Sedges (*Carex*) represent one of the most important and yet overlooked elements of the flora of fens. Herbarium specimens were examined at various institutions throughout Ohio, and field surveys were conducted at the majority of known fens in the state in 1990-1993. Based on these surveys, twenty-two species of sedges were deemed characteristic of Ohio fens. The occurrence of these twenty-two species was documented at twenty-seven of the most intact fens in Ohio. Maps were prepared recording known occurrences of these species in Ohio. The floristic affinities of the twenty-two Ohio fen sedges was determined based on state-wide and North American distribution as well as on occurrence in wetlands other than fens in Ohio. Ohio fens contain sedges of boreal as well as prairie affinity. Some species are obligate calciphiles which only occur in calcareous fens or on exposed limestone or dolomite bedrock.

INTRODUCTION

Peat-accumulating wetlands in Ohio have been designated as bog or fen based on hydrology, water pH, and vegetation (Andreas 1985). Ohio bogs have little flow of water, a pH between 3.5-5.5, a *Sphagnum* dominated ground layer, and an ericaceous shrub layer. Fens receive water from artesian springs or seeps, have a calcareous substrate, a pH between 5.5-8.0, and support minerotrophic species of bryophytes, sedges, composites and grasses. Ohio fens are usually characterized by a zone of shrubby cinquefoil (*Potentilla fruticosa*). Ohio bogs are ombrotrophic to weakly minerotrophic peatlands and may be named "poor fens" in other regions. Ohio fens are strongly minerotrophic wetlands, and may be designated "rich fens" in other regions. Of the 114 peatlands listed by Andreas (1985), 58 were considered fens and 56 were bogs. Of these peatlands, 39 fens and 27 bogs are still in existence.

Throughout North America, rich fens can be placed into two major groups based on floristic affinities and geography (Schneider 1992). Prairie fens occur mostly in the midwestern United States, generally north of the southern limit of Pleistocene glaciation and south of the boreal tension zone which passes through Minnesota, Wisconsin, southern Michigan, and southern Ontario. Most of these fens occur in Ohio, southern Michigan, southern Ontario, northern Illinois and Indiana, southeastern Wisconsin, northern Iowa, as well as in south-central and northwestern Minnesota. Prairie fens are also in the unglaciated Ozark Mountains of Missouri. Much of the area where these fens occur corresponds to the tallgrass prairie region of North America and prairie fens share many plant species with seasonally wet, tallgrass prairies. Boreal fens occur to the north of the tension zone in the boreal forest regions of northern Minnesota and Michigan, as well as in Canada and the northeastern United States. These fens have many plant species with northern distributions and share species with northern coniferous, swamp forests.

Ohio lies to the south of the boreal tension zone in the eastern deciduous forest region. Tallgrass prairie occurred only in small pockets in the western half of Ohio in pre-settlement times. In Ohio, Stuckey and Denny (1981) designated and mapped two types of fens (Figure 1). The prairie fens of west-central and south-central Ohio share a number of plant species with the tallgrass prairies of midwestern North America. Stuckey and Denny (1981) identified twenty plant species which were designated as the southeastern prairie element. These species also occur in wet prairies south of the limit of Pleistocene glaciation from the Appalachian Mountains westward to the Ozarks in Missouri. Examples of these species include: big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), Riddell's goldenrod (*Solidago riddellii*), queen-of-the-prairie (*Filipendula rubra*), blazing star (*Liatris spicata*), prairie loosestrife (*Lysimachia quadriflora*), nodding wild onion (*Allium cernuum*), winged loosestrife (*Lythrum alatum*), prairie dock (*Silphium terebinthinaceum*), whorled rosinweed (*Silphium trifoliatum*) and low nut-rush (*Scleria verticillata*).

The fens of northeastern Ohio, which Stuckey and Denny (1981) called "bog fens," share species with Ohio bogs and with the fens north of the boreal tension zone. Many of these species have northern distributions, but also occur in the Appalachian Mountains and on the Atlantic Coastal Plain. Some characteristic northeastern Ohio fen species are: swamp birch (*Betula pumila*), pitcher plant (*Sarracenia purpurea*), speckled alder (*Alnus rugosa*), tamarack (*Larix laricina*), poison sumac (*Toxicodendron vernix*), cranberry (*Vaccinium macrocarpon*), alder-leaved buckthorn (*Rhamnus alnifolia*), hoary willow (*Salix candida*), green cottongrass (*Eriophorum viridi-carinatum*) and white beak-rush (*Rhynchospora alba*). These fens also contain some species more typical of prairies and are floristically transitional be-

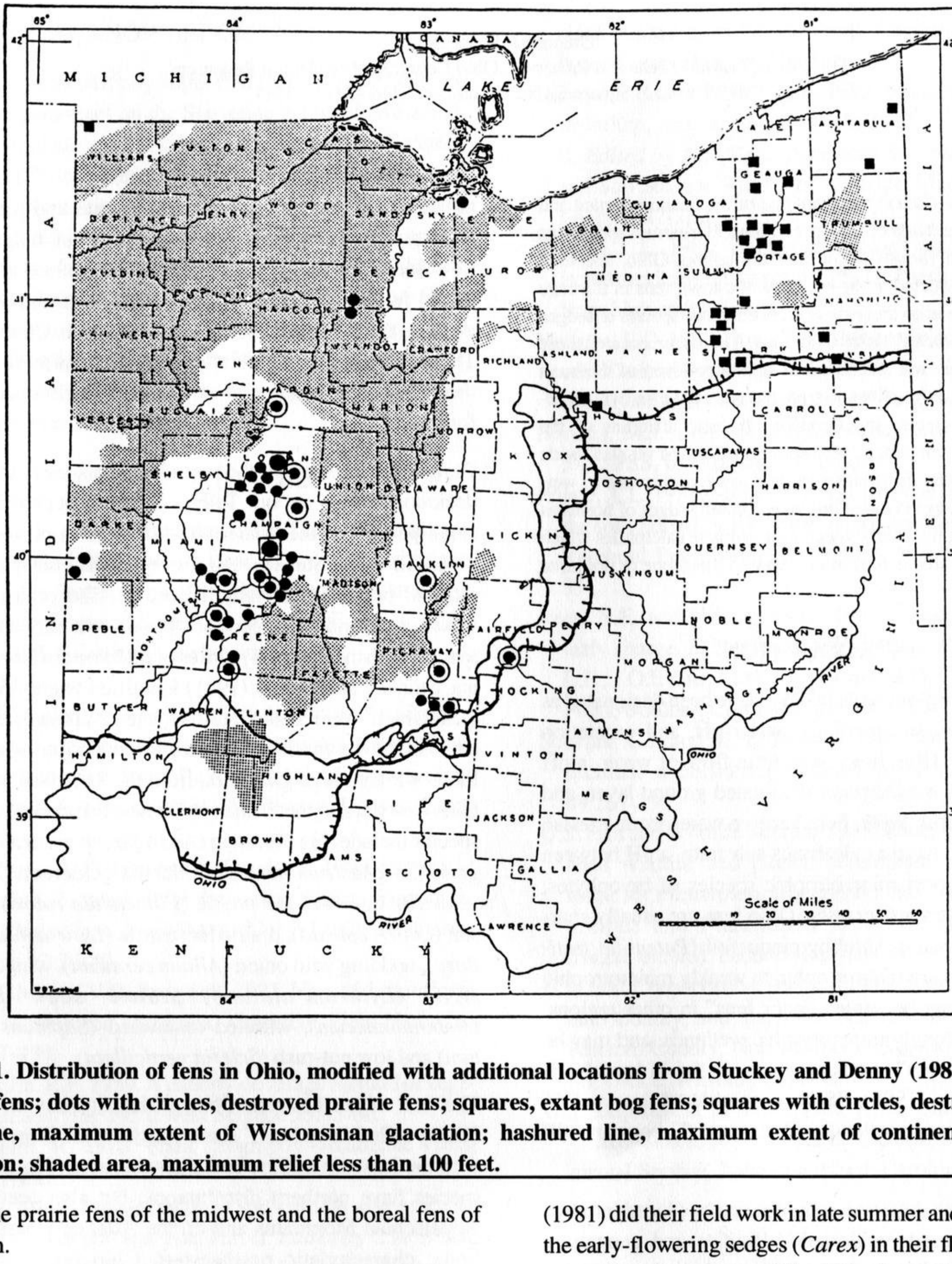
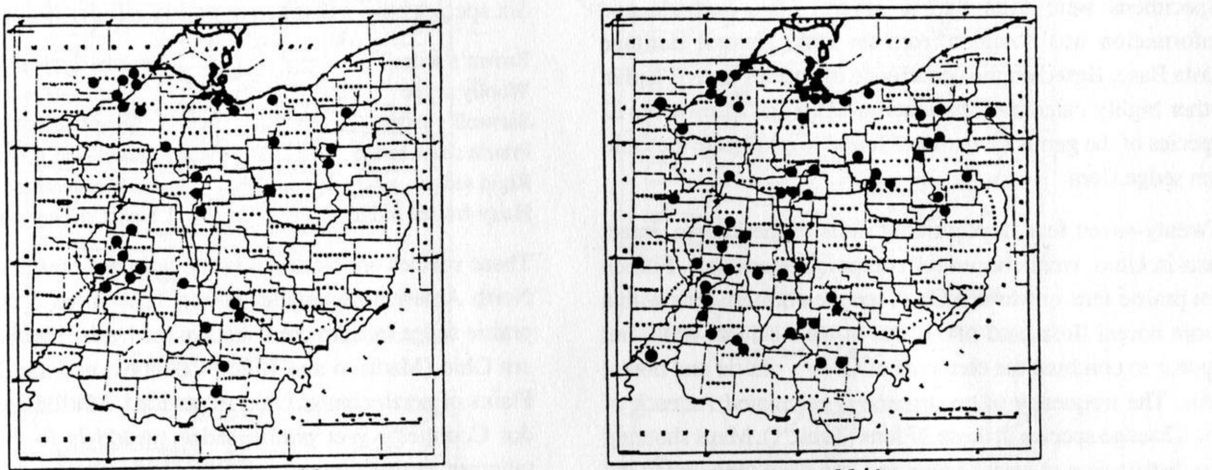


Figure 1. Distribution of fens in Ohio, modified with additional locations from Stuckey and Denny (1981). Dots, extant prairie fens; dots with circles, destroyed prairie fens; squares, extant bog fens; squares with circles, destroyed bog fens; solid line, maximum extent of Wisconsinan glaciation; hashured line, maximum extent of continental Pleistocene glaciation; shaded area, maximum relief less than 100 feet.

tween the prairie fens of the midwest and the boreal fens of the north.

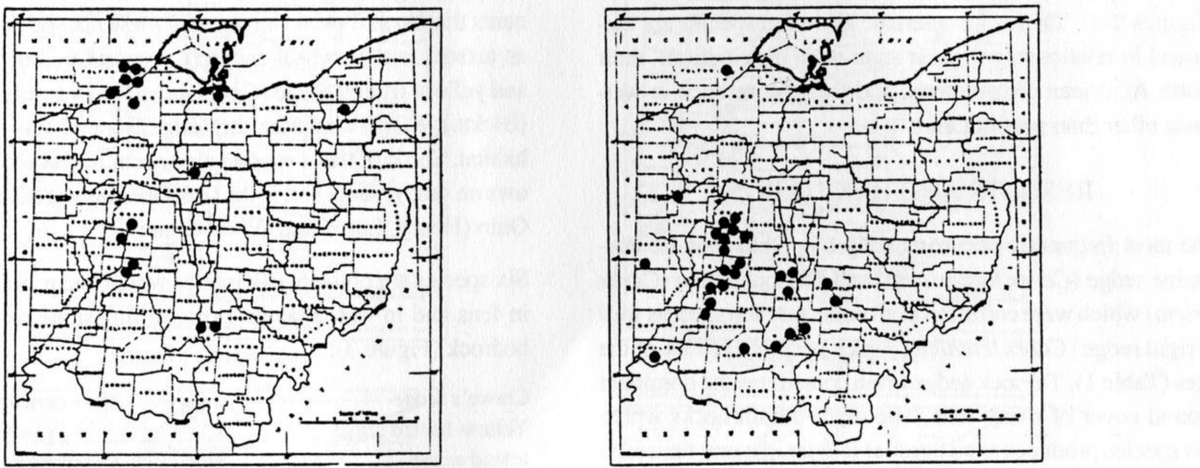
Many species which occur in fens in Ohio are also present in sedge meadows in the Oak Openings of Fulton, Henry, Lucas and Wood Counties of northwestern Ohio. The Oak Openings is an area characterized by sand deposits from preglacial Lake Warren underlain by limestone bedrock. Sedge meadows occur in areas where the water table is close to the surface creating a permanently saturated, calcareous substrate.

Despite the fact that sedges (*Carex*) are among the dominant plant species in fens, little has appeared in print to characterize this aspect of Ohio's flora. Since Stuckey and Denny (1981) did their field work in late summer and did not include the early-flowering sedges (*Carex*) in their floristic study, no comprehensive survey of the Ohio fen sedge flora had ever been compiled. Most sedges which typically occur in Ohio fens were underreported in Braun's *Monocotyledoneae* [of Ohio] 1967, reflecting the lack of sedge collections from Ohio fens. Many species which occur in these alkaline peatlands, including sedges, have narrow ecological tolerances and are restricted to fens or other highly alkaline habitats in the midwestern part of their ranges. These species may be rare or endangered in many regions as a result of widespread habitat destruction.



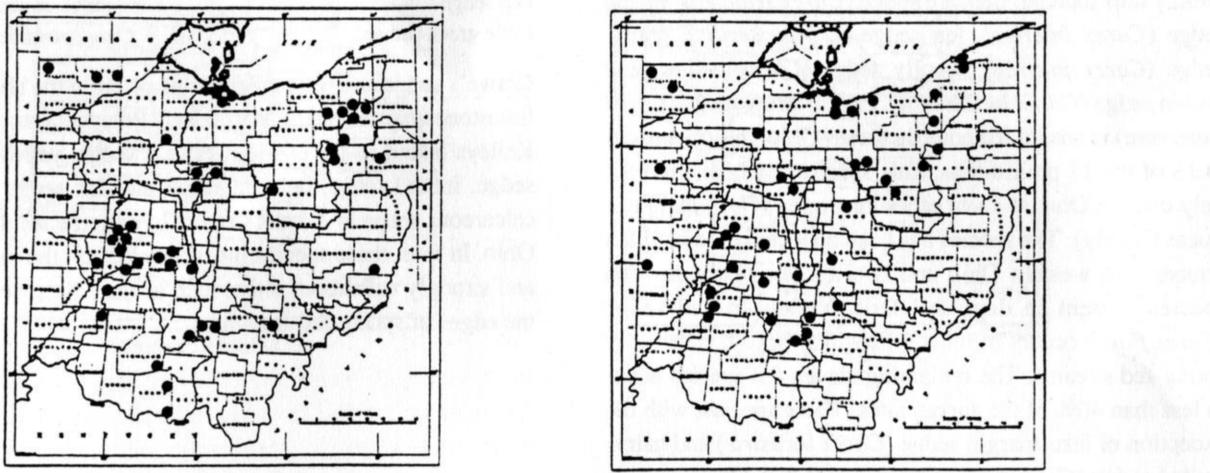
Carex buxbaumii

Carex pellita



Carex sartwellii

Carex suberecta



Carex tetanica

Carex trichocarpa

Figure 2. Species of prairie affinity.

OBJECTIVES AND METHODS

This study determines which species of sedges are characteristic of Ohio fens. Surveys were conducted during the 1990-93 field seasons at the majority of known fen sites. Specimens were examined at several Ohio herbaria and information was obtained from the Ohio Natural Heritage Data Base. Based on the occurrence of species in fens and in other highly calcareous habitats in Ohio and elsewhere, 22 species of the genus *Carex* were found to constitute the Ohio fen sedge flora.

Twenty-seven fens, representing most of the known, intact fens in Ohio, were chosen for comparative analysis. Fifteen are prairie fens in western Ohio, ten are northern fens with a more boreal flora, and two occur in west-central Ohio, but appear to combine the elements of Ohio's prairie and boreal fens. The frequency of occurrence is calculated for each of the 22 sedge species in these 27 fens (Table 1). Maps showing the distribution of each species in Ohio were prepared to aid in the analysis of geographic distributions and affinities (Figures 2-5). These characteristic Ohio fen species are discussed in relationship to their state-wide distributions, their North American distributions, and their occurrence in wetlands other than fens in Ohio.

RESULTS AND DISCUSSION

The most frequently occurring sedges in Ohio fens are Porcupine sedge (*Carex hystericina*) and Tussock sedge (*Carex stricta*) which were collected at all twenty-seven sites, as well as rigid sedge (*Carex tetanica*), which occurred at 93% of the sites (Table 1). Tussock sedge often constitutes the dominant ground cover of many fens. The uneven hummocks which this species produces are a familiar feature in many fen sedge meadows. Other species which occur in the majority of Ohio's fens include: delicate sedge (*Carex leptalea*), inland sedge (*Carex interior*), fen sedge (*Carex sterilis*), prairie sedge (*Carex prairea*), woolly sedge (*Carex pellita*) and brown sedge (*Carex buxbaumii*). Prairie straw sedge (*Carex suberecta*) is absent from northeastern Ohio, but does occur in 13 of the 17 prairie fens. This species has been reported only once in Ohio at a site other than a fen (Oak Openings, Lucas County). The species has been collected in several fen remnants in western Ohio and is often one of the last fen species present in degraded fens. Yellow-fruited sedge (*Carex flava*) occurs in most fens which have fast moving, spring-fed streams. The remaining eleven fen species occur in less than 40% of the survey sites. These species, with the exception of lake-margin sedge (*Carex lacustris*) and hairy-fruited sedge (*Carex trichocarpa*), are rare in Ohio.

Curtis (1959) considered fens to be a "hybrid community" which combines northern, atlantic coastal plain and prairie floristic elements. The twenty-two sedge species were placed into categories based on their occurrence in wetlands other than fens in Ohio and throughout North America in order to determine their floristic affinities.

Six species have a distinctive prairie affinity (Figure 2):

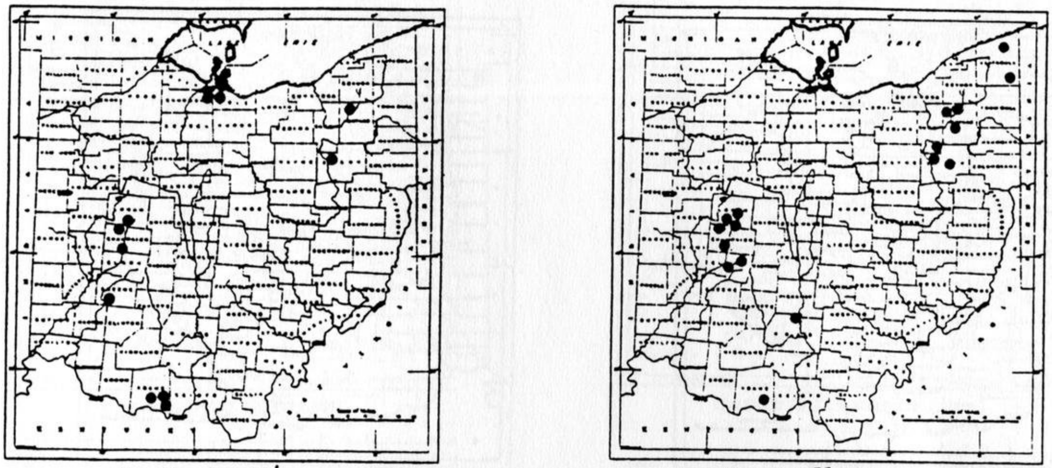
Brown's sedge	*Carex buxbaumii* Wahlenb.
Woolly sedge	*Carex pellita* Muhl.
Sartwell's sedge	*Carex sartwellii* Dewey
Prairie straw sedge	*Carex suberecta* (Olney) Britt.
Rigid sedge	*Carex tetanica* Schkuhr
Hairy-fruited sedge	*Carex trichocarpa* Muhl.

These species are common in the tallgrass prairie region of North America (Schneider 1992). They often occur in wet prairie sedge meadow remnants in the Darby Plains of western Ohio (Madison and Union Counties) and the Sandusky Plains of north-central Ohio (Crawford, Marion and Wyandot Counties). Wet prairie sedge meadows in the former tallgrass prairie regions of Ohio have almost completely disappeared. However, recent surveys of the few, small remnants that do still exist suggest that these six species, as well as tussock sedge, wheat sedge (*Carex atherodes* Sprengel) and yellow-fruited sedge (*Carex annectens* var. *xanthocarpa* (Bickn.) Wieg.) comprise the sedge flora of this imperiled habitat. Some of these species also occur in wet sedge meadows on sandy, peaty soil in the Oak Openings of northwestern Ohio (Henry, Lucas and Wood Counties).

Six species are obligate calciphiles which occur in Ohio only in fens and in wet areas on exposed limestone or dolomite bedrock (Figure 3):

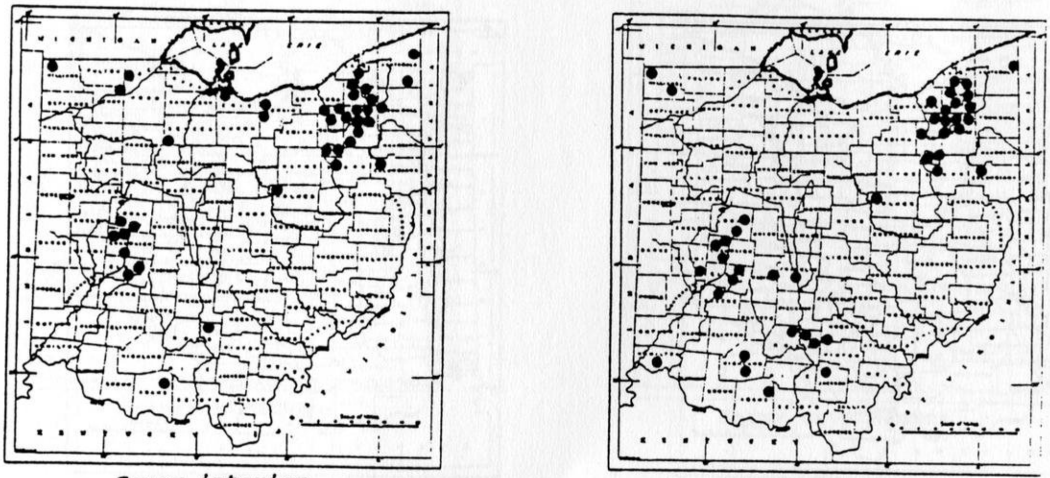
Crawe's sedge	*Carex crawei* Dewey
Yellow-fruited sedge	*Carex flava* L.
Inland sedge	*Carex interior* Bailey
Delicate sedge	*Carex leptalea* Wahlenb.
Fen sedge	*Carex sterilis* Willd.
Little green sedge	*Carex viridula* Michx.

Crawe's sedge and little green sedge occur in the abandoned limestone quarries on the Marblehead Peninsula and adjacent Kelleys Island in Lake Erie. Crawe's sedge, yellow-fruited sedge, inland sedge, delicate sedge and fen sedge grow in calcareous seeps in Adams County of extreme south-central Ohio. In fens, these species invariably inhabit the most open and strongly calcareous sites, such as marl flats, seeps, and the edges of spring-fed streams.



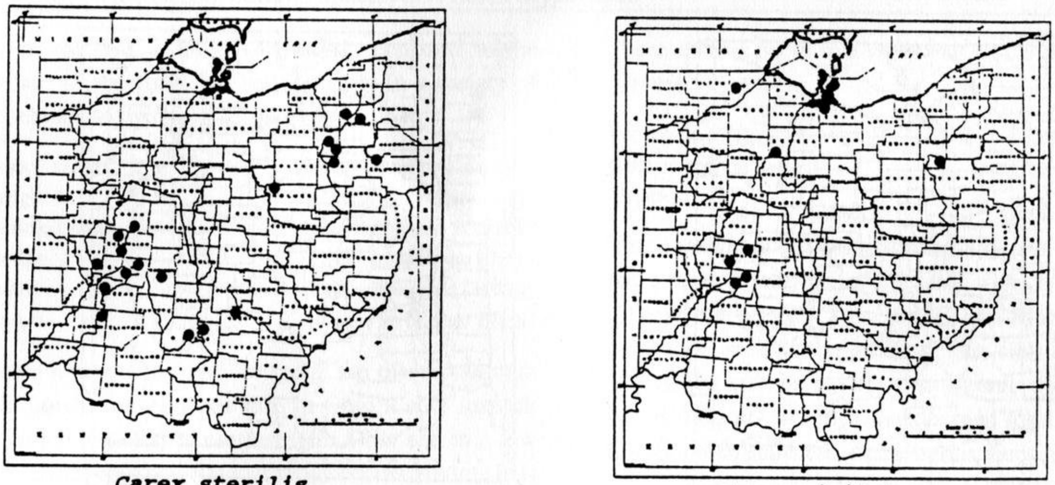
Carex crawei

Carex flava



Carex interior

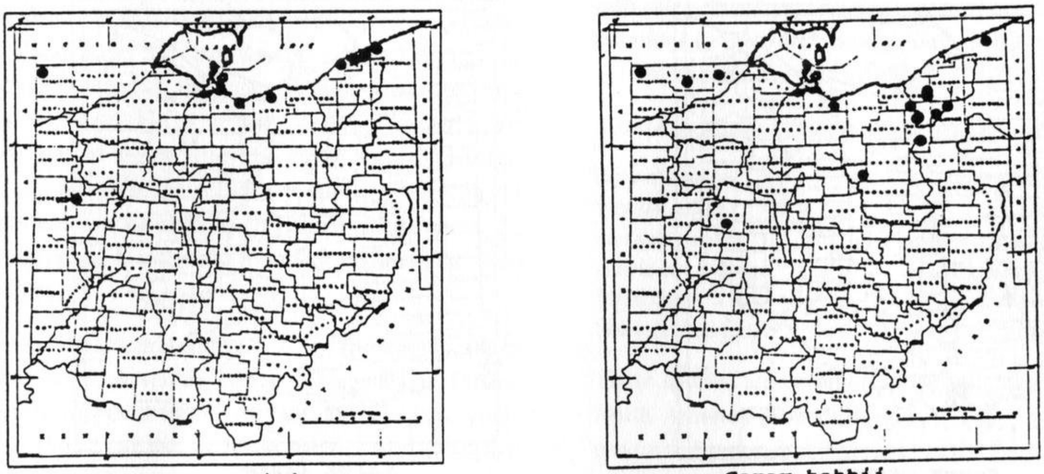
Carex leptalea



Carex sterilis

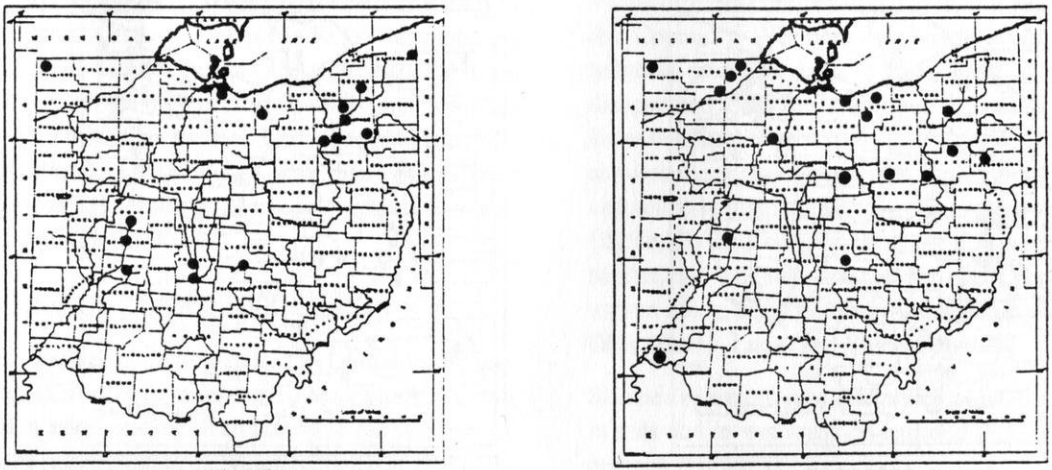
Carex viridula

Figure 3. Species of fens and calcareous bedrock.



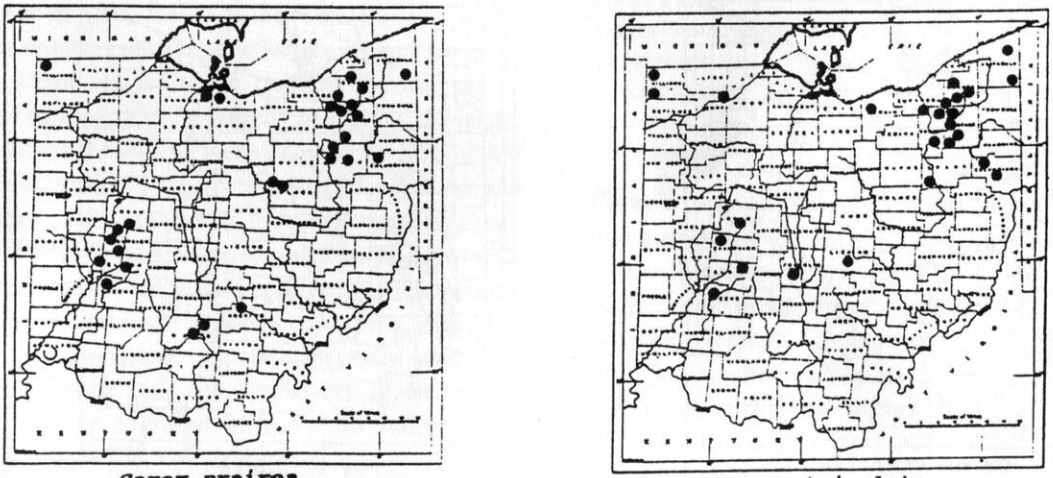
Carex aquatilis

Carex bebbii



Carex diandra

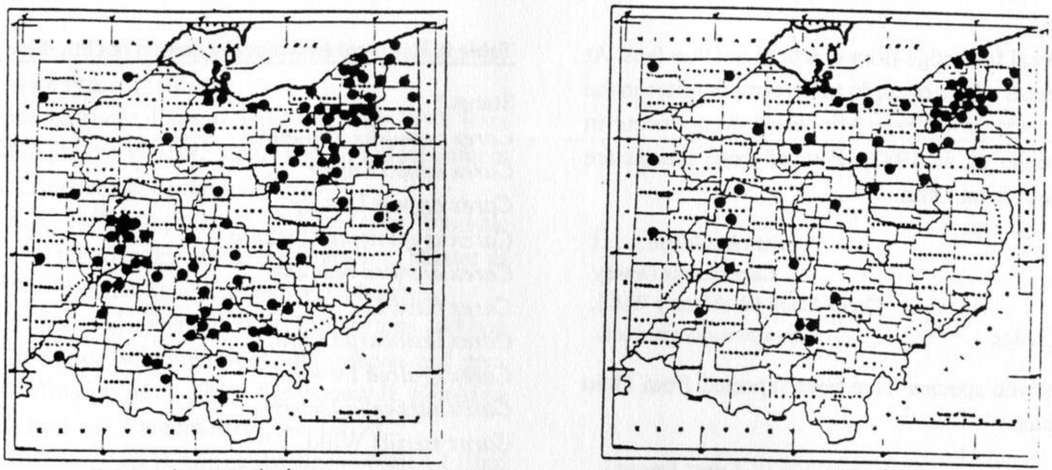
Carex lasiocarpa



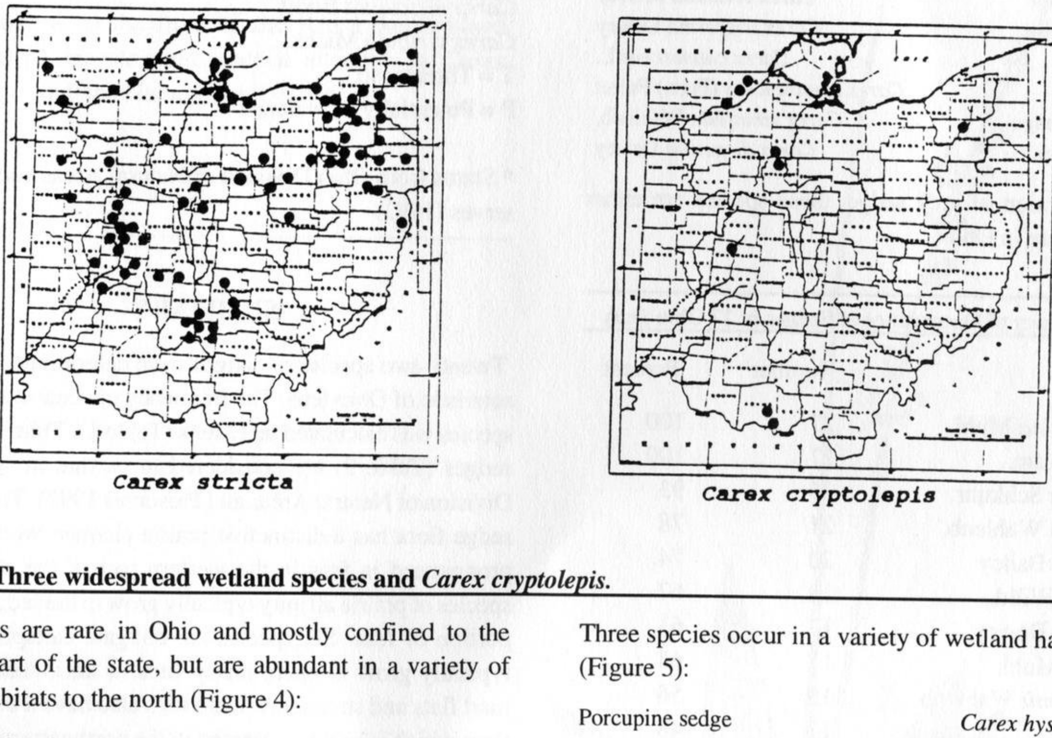
Carex prairea

Carex utriculata

Figure 4. Fen species abundant in a variety of wetlands north of Ohio.



Carex hystericina ***Carex lacustris***



Carex stricta ***Carex cryptolepis***

Figure 5. Three widespread wetland species and *Carex cryptolepis*.

Six species are rare in Ohio and mostly confined to the northern part of the state, but are abundant in a variety of wetland habitats to the north (Figure 4):

Leafy tussock sedge	*Carex aquatilis* Wahlenb.
Bebb's sedge	*Carex bebbii* Olney
Lesser panicled sedge	*Carex diandra* Schrank
Slender sedge	*Carex lasiocarpa* Ehrh.
Prairie sedge	*Carex prairea* Dewey
Beaked sedge	*Carex utriculata* Boott

Leafy tussock sedge and slender sedge are often dominant species in boreal fens, but are rare in Ohio. Leafy tussock sedge occurs in one fen in northwestern Ohio and in a few Lake Erie coastal marshes. Slender sedge occurs in some fens and bogs, but is never a dominant species. It also occurs in sedge meadows in the Oak Openings of northwestern Ohio. Bebb's sedge, lesser panicled sedge, prairie sedge and beaked sedge sometimes inhabit Ohio bogs, as well as fens. These six species represent the boreal element which is more characteristic of northern Ohio fens.

Three species occur in a variety of wetland habitats in Ohio (Figure 5):

Porcupine sedge	*Carex hystericina* Muhl.
Lake-margin sedge	*Carex lacustris* Willd.
Tussock sedge	*Carex stricta* Lam.

These species are extremely abundant in Ohio, but mostly in the glaciated portions of the state. One additional species, little yellow sedge (*Carex cryptolepis* Mackenz.), regularly occurs on sandy, somewhat acidic sites (Crins and Ball 1989). The species is known from only three fens in Ohio, but also occurs in sedge meadows in the Oak Openings. It has also been collected in calcareous seeps in Adams County.

Much of the boreal fen sedge flora is absent in Ohio fens. At least eleven species which occur in minerotrophic sites in the Red Lake Peatlands of northern Minnesota do not occur in Ohio fens (Wheeler et. al. 1983). Four of these species are completely absent from Ohio:

Creeping sedge	*Carex chordorrhiza* L.f
Meager sedge	*Carex exilis* Dewey
Pale sedge	*Carex livida* (Wahlenb.) Willd.
Smaller bearded sedge	*Carex pseudocyperus* L.

An additional seven species have been reported from Ohio bogs, but not fens:

Mud sedge	*Carex limosa* L.
Little prickly sedge	*Carex echinata* Murray
Three-seeded sedge	*Carex trisperma* Dewey
Grey sedge	*Carex cannescens* L.
Brownish sedge	*Carex brunnescens* (Pers.) Poiret
Thin-flowered sedge	*Carex tenuifolia* Wahlenb.
Two-seeded sedge	*Carex disperma* Dewey

With the exception of grey sedge, these species are either extirpated or rare in Ohio.

Table 1. Frequency of Occurrence of Sedges in 27 Ohio Fens

Species	Number	Percent
Carex hystericina Muhl.	27	100
Carex stricta Lam.	27	100
Carex tetanica Schkuhr.	25	93
Carex leptalea Wahlenb.	21	78
Carex interior Bailey	20	74
Carex sterilis Willd.	18	67
Carex prairea Dewey	17	63
Carex pellita Muhl.	17	63
Carex buxbaumii Wahlenb.	15	56
Carex flava L.	13	48
Carex suberecta (Olney) Britt.	13	48
Carex lacustris Willd.	10	37
Carex sartwellii Dewey	9	33
Carex utriculata Boott	8	30
Carex viridula Michx.	7	26
Carex trichocarpa Muhl.	6	22
Carex lasiocarpa Ehrh.	5	19
Carex diandra Schrank	5	19
Carex crawei Dewey	4	15
Carex cryptolepis Mackenz.	4	15
Carex bebbii Olney	4	15
Carex aquatilis Wahlenb.	1	4

Table 2. Rare and Endangered Sedges of Ohio Fens

	Status *
Carex aquatilis Wahlenb.	T
Carex bebbii Olney.	T
Carex crawei Dewey	P
Carex cryptolepis Mackenz.	P
Carex diandra Schrank	P
Carex flava L.	P
Carex lasiocarpa Ehrh.	T
Carex prairea Dewey	P
Carex sartwellii Dewey	T
Carex sterilis Willd.	P
Carex suberecta (Olney) Britt.	P
Carex utriculata Boott	P
Carex viridula Michx.	P

T = Threatened
P = Potentially Threatened

* Status from Ohio Division of Natural Areas and Preserves (1992)

SUMMARY

Twenty-two species of sedges were determined to be characteristic of Ohio fens. The frequency of occurrence of these species was calculated at 27 fens (Table 1). Thirteen of these sedges (Table 2) are considered to be rare in Ohio (Ohio Division of Natural Areas and Preserves 1992). The Ohio fen sedge flora has a distinctive prairie element which is more pronounced in fens in the western part of the state. These species of prairie affinity typically grow in the sedge meadow portion of fens. Six species are obligate calciphiles which typically grow in open, marly sites in fens, such as seeps, marl flats and streamlets. Ohio fens also have a boreal sedge flora which is best represented in the northeastern part of the state. However, much of the boreal sedge flora of North America is absent from Ohio fens.

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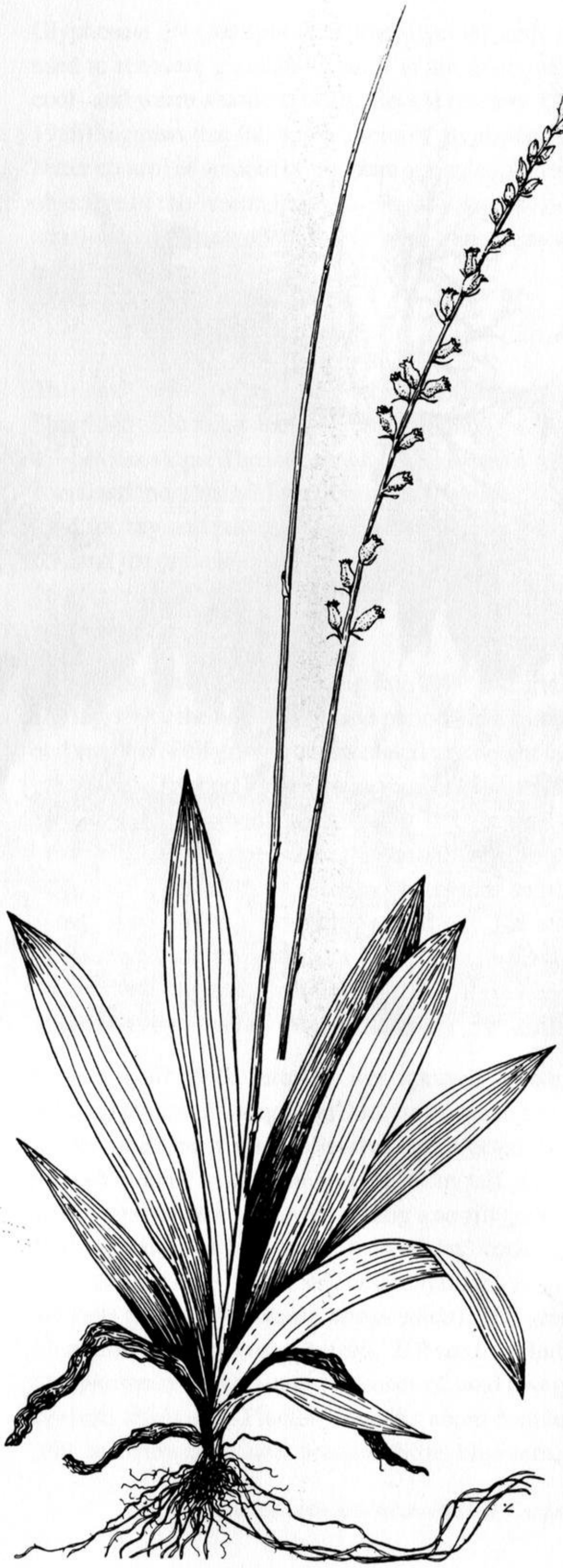

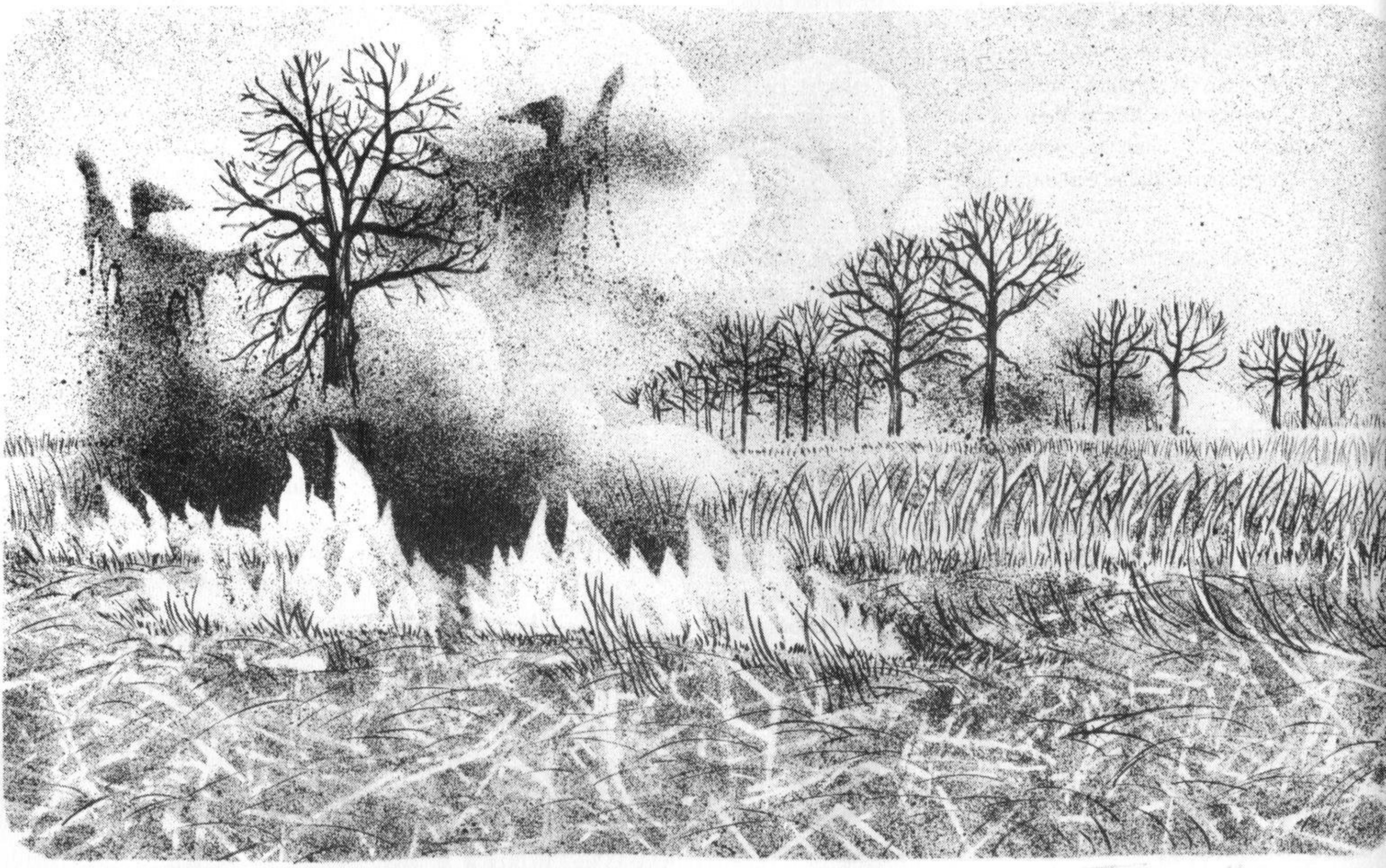

CONVERTING SMOOTH BROME PASTURE TO WARM-SEASON GRASSES

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Abstract. Smooth brome (*Bromis inermis*) is a cool-season grass that currently dominates many grasslands. Restoring warm-season grasses to some grasslands would improve season-long grazing and wildlife habitat. A 2x2x2x2 factorial of treatments with or without fall glyphosate [*N*-(phosphonomethyl)glycine] (0.56 kg/ha), spring atrazine [2-chloro-4-(ethylamino)-6-(isopropylamino)-s-triazine] (2.24 kg/ha), spring burning, and spring sod-seeding of a mixture of big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), sideoats grama (*Bouteloua curtipendula*), Indian grass (*Sorghastrum nutans*), and sand lovegrass (*Eragrostis trichodes*) was applied in three replications to a smooth brome sod. Burning had little effect, partly due to low fuel load. Fall glyphosate killed smooth brome more effectively than did spring atrazine, but atrazine controlled annual weeds better than glyphosate. Slow, uneven, but eventually acceptable stands were developing where either herbicide was used alone. Using both herbicides nearly eliminated biomass of competing species for one growing season and permitted atrazine-tolerant, warm-season grasses to become established and ready to graze by the second year.

INTRODUCTION

Smooth brome (*Bromis inermis*) is an introduced, cool-season grass that currently dominates many prairie grasslands in central USA. In most areas of north central and northeastern USA, smooth brome and other cool-season grasses are the primary grazing resource.

Smooth brome often produces over 50 percent of its annual growth prior to June. Summer growth of smooth brome often is minimal and the resulting forage is low quality. Livestock grazing smooth brome during summer usually experience much poorer performance compared to either spring performance when grazing smooth brome or summer performance when grazing warm-season grasses (Anderson 1988).

Season-long performance of grazing livestock is better when separate pastures of cool-season and warm-season grasses are available for grazing rather than having only one type of grass available (Anderson 1988). Warm-season grasses also are preferred over smooth brome by most wildlife.

Atrazine [2-chloro-4-(ethylamino)-6-(isopropylamino)-s-triazine] is phytotoxic to most cool-season species (Houston 1977). However, some warm-season grasses tolerate atrazine at time of establishment (Martin et al. 1982), and several studies have used atrazine to successfully renovate warm-season grasslands (Samson and Moser 1982, Waller and Schmidt 1983, Dill et al. 1986). However, atrazine can no longer be used legally on grasslands except in a few situations.

Glyphosate [*N*-(phosphonomethyl)glycine] also has been used to renovate grasslands, but it is not selective between cool- and warm-season species. Recent research (Anderson 1986) suggests that fall applications of glyphosate may give better control of smooth brome than spring applications. The objective of this research was to compare ways besides using atrazine to replace smooth brome with warm-season grasses using no tillage.

METHODS

This study was conducted six km east of Lincoln, NE on a Sharpsburg silty clay loam (Typic Argiudoll) with less than a 3 percent slope. The site contained an established sod that contained more than 95 percent smooth brome and had been used for hay and pasture for at least ten years. Soil pH was 6.4, and the organic matter, Bray-1 P, and K quantities were 26 g/kg, 6 mg/kg, and 374 mg/kg, respectively. No fertilizer was added during the study.

Treatments were applied during fall 1990 and spring 1991. During 1990, the site was grazed periodically during spring and summer. Fall growth accumulated to a height of 10 to 15 cm by mid-October. Following several evenings when night-time low temperatures were below 0 C in late October, randomly selected plots were sprayed with glyphosate at 0.56 kg/ha in a 2 percent w/w solution of ammonium sulfate and water. The solution was applied at 93 L/ha. The ammonium sulfate and relatively low water volume are important to help reduce chelating and deactivation of the active ingredient of glyphosate by minerals in the water.

In mid-April 1991, atrazine was sprayed onto randomly selected plots at 2.24 kg/ha in 93 L/ha of water. In late April, a prescribed burn was conducted on selected plots when smooth brome was green and ca 8 cm tall. In late May, selected plots were sod-seeded using a no-till grassland drill. Planting rate was 600 pure live seeds/m^2 consisting of 60 seeds each of little bluestem (*Schizachyrium scoparium*) and sideoats grama (*Bouteloua curtipendula*), 150 seeds of big bluestem (*Andropogon gerardii*), 210 seeds of Indian grass (*Sorghastrum nutans*), and 120 seeds of sand lovegrass (*Eragrostis trichodes*). Planting rate was about double the usually recommended rate because little bluestem, sideoats grama, and sand lovegrass were known to be sensitive to atrazine and were not expected to become established.

The experimental design was a randomized complete block with three replicates. The 2 x 2 x 2 x 2 factorial was arranged as a split-split-split plot, with spring burning as the whole plot, fall glyphosate as the sub plot, sod-seeding as the sub-sub plot, and spring atrazine as the sub-sub-sub plot. Data were analyzed using ANOVA and GLM procedures (SAS 1988). Mean comparisons were made using a protected LSD test with a 5% level of significance.

All plots were shredded to a stubble height of 20 cm to reduce competition from common ragweed (*Ambrosia artemisiifolia*) in August 1991. In June 1992, 0.56 kg/ha of 2,4-D [2,4-dichlorophenoxyacetic acid] was applied in 186 L/ha of water for control of numerous broadleaf weeds.

Yield (above-ground live biomass) was estimated by hand clipping two quadrats (0.6 m^2) per plot at ground level 60 days (late July 1991) following sod-seeding and at 5 cm above ground level at 120 (late September 1991) and 420 (mid-July 1992) days following sod-seeding. Dead material was discarded at all harvests, and at 120 and 420 days the live biomass was separated into seeded species and other species. Samples were dried in a forced-air oven for 72 hours at 60 C and weighed.

RESULTS AND DISCUSSION

Initial Biomass Control

Spring atrazine was effective at reducing initial biomass of competing species 60 days after sod-seeding (315 vs 1045 kg/ha for atrazine-treated and untreated plots averaged across all other treatments, respectively) (Table 1). Annual weeds were virtually eliminated in July, and smooth brome was severely suppressed, although many plants did recover and grow aggressively the next year. This agrees with other studies that have shown that atrazine will control many annual weeds as well as kill or weaken cool-season grasses like smooth brome (Samson and Moser 1982, Waller and Schmidt 1983, Dill et al. 1986).

Glyphosate-treated plots also had much less biomass in July to compete with new seedlings following sod-seeding than did untreated plots (350 vs 1010 kg/ha, respectively, averaged across all other treatments). Most growth in glyphosate-treated plots was from annual weeds. Since this smooth brome sod originally had low weed populations, sods with high weed populations might produce more biomass and competition from weeds unless other weed control practices are used.

Some smooth brome plants also survived in plots treated with glyphosate. Surviving plants eventually regained vigorous growth and contributed substantial biomass the next year, especially in plots that were not treated with atrazine also. Previous research (Anderson 1986) reported almost complete killing of smooth brome treated with glyphosate in late fall, probably due to effective translocation into the root system. Dry growing conditions during fall of 1990 may have reduced plant uptake of glyphosate and reduced its effectiveness.

Glyphosate was applied in late October after several nights of below freezing temperatures. Observations suggested that warm-season grasses that had become dormant due to freezing temperatures would not be affected by glyphosate. It was hoped that some remnant warm-season grasses might be present in the sward that would grow vigorously the next year due to lessened competition. Unfortunately, only two switchgrass (*Panicum virgatum*) and five dropseed (*Sporobolus* spp.) plants were present in the entire study area the next year. As a result, only sod-seeded plots had production of seeded species. Thus, no data were collected from plots that were not sod-seeded.

On burned plots, green spring growth of smooth brome burned poorly because of a low fuel load. As a result, burning had little impact on the yield of live biomass (Table 1).

There was a significant burn by glyphosate interaction. Although burning did not reduce biomass compared to not burning when averaged across all treatments, there was a trend for burning to be beneficial when glyphosate was used the previous fall and atrazine was not applied. Glyphosate-treated plots burned more thoroughly than untreated plots. This burning may have weakened or killed some surviving smooth brome plants as well as early emerging weeds. This interaction suggests that burning may be beneficial and more effective than occurred in this study whenever sufficient fuel is available to have a thorough burn.

Establishment

Seeded warm-season grasses produced no harvestable growth by the end of the first growing season (120 days following sod-seeding) on plots that had not been sprayed with glyphosate or atrazine (Table 1). This probably was due to excessive competition by the live biomass of other species throughout the season.

Plots treated with both atrazine and glyphosate produced less than 40 percent of the total biomass of plots that had no herbicide treatments by the end of the first growing season. However, while all the biomass of untreated plots was smooth brome and weeds, plots treated with atrazine and glyphosate yielded an average of 680 kg/ha of the seeded species and only 50 kg/ha of other biomass from other species. Excellent stands were present and seedlings ap-

Table 1. Dry matter yield of biomass and seeded species 60, 120, and 420 days after sod-seeding into a smooth brome sod sprayed with glyphosate or atrazine or burned.

			Days after sod-seeding				
Treatments			60	120		420	
Glyphosate	Atrazine	Burn	Biomass	Biomass	Seeded species	Biomass	Seeded species
---------- kg/ha -------------			---------- kg/ha ----------				
0.56	2.2	yes	20	710	690	1840	1390
0.56	2.2	no	60	750	670	1760	1270
0.56	0	yes	420	650	260	1360	820
0.56	0	no	900	1030	180	1580	600
0	2.2	yes	570	680	100	1290	520
0	2.2	no	610	900	160	1450	640
0	0	yes	1370	1970	0	1150	400
0	0	no	1490	1810	0	1330	320
LSD (0.05)			337	451	266	195	307

peared healthy and vigorous. Although species separations were not made, it was visually obvious that most seedlings were big bluestem and Indian grass. This was expected, due to the variable tolerance of species to atrazine at time of seeding (Martin et al. 1982). Indian grass had more plants than might have been expected, based on its partial sensitivity to atrazine, but the six-week interval between atrazine application and seeding may have reduced atrazine toxicity sufficiently to allow Indian grass seedlings to tolerate the atrazine concentration still present.

Plots treated with either atrazine or glyphosate, but not both, produced 100 to 260 kg/ha of the seeded species during the first growing season. From 390 to 850 kg/ha of competing biomass also was present in these plots after 120 days. Glyphosate-treated plots had plants of all five seeded species, but only big bluestem and Indian grass were found in atrazine-treated plots.

By mid-July of the second year (420 days after sod-seeding), yield of the seeded species on plots treated with both atrazine and glyphosate was equal to the total biomass yield on untreated plots, and total biomass on these treated plots was at least 30 percent greater than on untreated plots. Sufficient growth and vigor of seeded grasses was available for moderate grazing. Seeded grasses in plots treated with only one herbicide were well established, although growth was uneven and erratic. Growth still was insufficient for grazing, but stands were developing so that grazing could begin next year.

CONCLUSIONS

Sod-seeding warm-season grasses into smooth brome or other cool-season grass sod requires control of competing species from the existing sod. Spraying the sod with glyphosate in the fall and atrazine the following spring nearly eliminated all biomass of competing species for one growing season. This permitted excellent stands of warm-season grasses tolerant to atrazine to develop that were ready for grazing within one year.

Spraying with glyphosate in the fall controlled biomass of competing species as effectively as spraying atrazine in the spring when either herbicide was used alone. Glyphosate was more effective on smooth brome than was atrazine, but atrazine controlled many annual weeds that glyphosate did not control. Since atrazine currently has limited legal use on grasslands due to environmental concerns, the fall glyphosate treatment may be an effective substitute on grasslands that do not have a high annual weed potential. It may take longer for seeded species to establish well enough to be grazed than when using both glyphosate and atrazine, but glyphosate-treated sods will not restrict warm-season grass seedling diversity as did atrazine. Glyphosate also can control smooth brome in warm-season grasslands during late fall when desirable warm-season grasses are dormant but smooth brome is still green and susceptible.

Prescribed burning did not control biomass nor aid establishment in this study, but interactions with glyphosate suggested that low fuel load may have hindered its effectiveness.

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BUCKTHORN CONTROL WITH GARLON 3A AT PIPESTONE NATIONAL MONUMENT

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Abstract. Common buckthorn (*Rhamnus cathartica* L.) is a deciduous shrub or small tree introduced to the United States from northern Europe. It invades oak savanna and woodland in the upper Midwest. Methods of controlling buckthorn were investigated during early June and September 1986 at Pipestone National Monument, Minnesota. Control plots were compared with Garlon 3A stump (44.4 percent triclopyr) and foliar treatments (106.1 g/3.8 L water). Stump treatments in June and September killed 100% of buckthorn resprouts. Foliar treatment in June killed more resprouts than foliar treatment in September although both were not 100% effective. Results indicate that late season foliar treatment of buckthorn resprouts should be avoided due to a low mortality rate.

INTRODUCTION

As Europeans settled in the United States, they often planted common buckthorn (*Rhamnus cathartica* L.) in hedgerows around their homes (Bailey 1976). As early as 1849, buckthorn was being recommended as a hedge plant for Wisconsin farmsteads (Gourley 1985). Over time, this shrub or small tree, which is native to northern Europe and well adapted to the continental climate of southern Minnesota, central South Dakota, and southern Wisconsin, spread and became a common understory component of oak woods and savanna (Soper and Heinburger 1982).

At Pipestone National Monument (PNM) in southwestern Minnesota, buckthorn grows from three to six meters in height and invades both riparian woods and oak savanna (Becker 1986). In the early 1980s, park personnel surveyed buckthorn infested areas to determine an age distribution for the population. They found the oldest specimen was 33 years old, while most individuals were 10-20 years old. Although buckthorn was a relatively recent addition to the park flora, it dominated the woodland understory and had decimated the native herbaceous plants in the oak savanna.

In 1984, park personnel initiated buckthorn control. Plants in the most heavily infested riparian areas of the park were cut at ground level. Some stumps were treated with Ammate (ammonium sulfamate) at the rate of 1.6 kg/3.8 L of water (3.5 lbs/gal.) and some were left untreated. All the untreated buckthorn resprouted, while 75 percent of the treated stumps also resprouted, perhaps because Ammate, which is a wettable powder, came out of solution.

Personnel at PNM also monitored the effects of spring prescribed burns on buckthorn. Burning top-killed mature buckthorn but resprouting occurred within a few days. Buckthorn seedlings, on the other hand, succumbed readily to fire, possibly because of a poorly developed root system. Unfortunately, buckthorn seedlings occur most often in areas with little litter to carry a fire.

Since these approaches did not work, the situation was reassessed and a new buckthorn control strategy planned. Herbicide labels were reviewed in order to identify a chemical which might be used as both a stump and foliar treatment. This was necessary because some buckthorn thickets were so dense that a person with a hand sprayer could not penetrate them. Aerial herbicide application was not an option because of the overstory of bur oak (*Quercus macrocarpa* Michx.) and green ash (*Fraxinus pennsylvanica* Marsh.). Therefore, these areas would need to be cut and stump treated.

Although no information could be found which showed Garlon 3A as a proven buckthorn control agent, it was selected because it was approved for both foliar and stump treatments. Other potentially effective herbicides such as Roundup (glyphosate) were considered but not selected because they were not stump approved at the time. Finally, the decision was made to determine an optimum season of the year to apply Garlon 3A. The seasonal periods tested were chosen in part by the availability of park personnel.

METHODS

In 1986, two 11.5 m x 11.5 m plots were established in dense thickets of buckthorn resprouts (Figure 1). These two areas had been stump cut the year before but not treated with a herbicide. The result was vigorous resprouting with stumps producing from 1 to 40 resprouts (Figure 2). In one season these resprouts had grown to 1 cm in diameter and a maximum height of 2 m. Brue (1980) noted similar vigorous resprouting of *R. frangula* in Wisconsin.

Resprout thickets were chosen for the tests because they covered a significant area of the park and potentially were more of a management concern than mature buckthorn thickets not previously cut.

Figure 1. Dense thicket of buckthorn resprouts from untreated stumps, Pipestone NM, 1986.

Each plot was subdivided into sixteen 2 x 2 m subplots separated by .5 m buffer lanes. Treatments were as follows: control (CON), Garlon spray June (GSJ), Garlon cut June (GCJ), Garlon spray September (GSS), and Garlon cut September (GCS). Treatments were randomly applied in each plot with three replications per herbicide treatment and four per control.

Buckthorn foliage was sprayed with Garlon 3A during early June and September at the rate of 106.1 g/3.8 L of water (3.75 oz./gal.) A backpack sprayer was used. Garlon 3A was applied with a spray bottle as a stump treatment in June and September using the chemical directly from the container without dilution. The Garlon 3A label directions for stump treatment were followed as closely as possible. Freshly cut resprout stumps were sprayed within 30 minutes making sure the cambium was completely wet but avoiding adjacent vegetation.

Figure 2. Buckthorn stump resprouts.

The plots were resurveyed in late spring 1987 and the number of dead resprouts counted.

The effect of herbicide treatments on buckthorn was assessed using one-way analysis of variance (ANOVA). Only plot 1 data were used in the analysis. Percent resprout mortality was the dependent variable. A square-root transformation was applied to stabilize the variance. Duncan's Multiple Range test was used for a pairwise comparison of treatment means.

RESULTS

Stump treatment of buckthorn resprouts with Garlon 3A in June and September killed 100% of the resprouts (Table 1). Foliar treatment in June killed 77-100% of the resprouts, whereas the September foliar treatment killed from 32-60% of the resprouts. All the resprouts in the control plots were alive in 1987.

For the plot 1 data, Duncan's Multiple Range Test showed significantly less resprout mortality with the GSS treatment as compared to the other herbicide treatments (Figure 3).

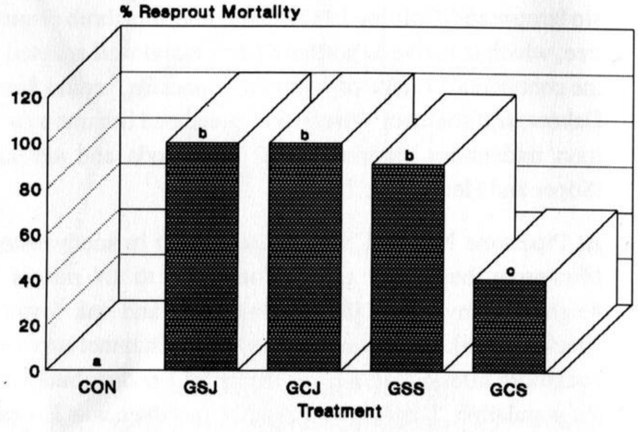

Figure 3. Buckthorn resprout mortality (%) following herbicide treatments in 1986 at Pipestone NM. Treatments having the same letter are not significantly different (P>.05) according to Duncan's multiple range test.

DISCUSSION

Several investigations have shown herbicides to be effective in controlling buckthorn. Kline (1983) found a stump application of 20% glyphosate in August/September to be 100% effective. She found glyphosate had little effect on non-target vegetation. However, at the time of this investigation glyphosate was not approved for commercial stump application. Kline (1983), also found 2,4-D(12.5%) in diesel fuel, 100% effective following basal application. However, Farrar

Table 1. Results of buckthorn treatment with Garlon 3A, plot 1 and 2, Pipestone NM, 1986.

	Plot 1			Plot 2		
Subplot	Number Resprouts[1]	Number Dead	Percent Dead	Number Resprouts	Number Dead	Percent Dead
CONTROL 1	*	0	0	*	0	0
CONTROL 2	*	0	0	*	0	0
CONTROL 3	*	0	0	*	0	0
CONTROL 4	*	0	0	*	0	0
Garlon Cut Stump June						
GCJ1	88	88	100	**	**	**
GCJ2	55	55	100	**	**	**
GCJ3	68	68	100	**	**	**
Garlon Cut Stump September						
GCS1	146	146	100	**	**	**
GCS2	60	60	100	**	**	**
GCS3	94	94	100	**	**	**
Garlon Foliar Spray June						
GSJ1	61	61	100	32	32	100
GSJ2	35	34	97	21	21	100
GSJ3	44	34	77	61	56	92
Garlon Foliar Spray September						
GSS1	46	22	48	36	17	47
GSS2	45	20	44	53	24	45
GSS3	25	8	32	43	26	60

*Not counted

**Not sampled, all sprouts were dead

[1] Total number of resprouts from all stumps cut in plot.

(1983) noted that Picloran + 2,4-D is soil mobile and probably affects non-target vegetation in certain areas.

Results of this investigation show Garlon 3A, applied as a stump treatment to cut resprouts, to be as effective as glyphosate and 2,4-D on first cut stumps. Early season foliar applications were almost as effective as the stump treatments. However, late season foliar treatment of resprouts was less effective and may not provide adequate buckthorn control.

Although not directly related to the objectives of the study, herbicide damage to non-target plants inside and outside the treatment plots was not observed. Furthermore, within three months after June cutting and herbicide treatment native plants began reappearing in the herbicide subplots (Table 2). These plants may have been present in the soil as seeds and rootstocks but suppressed by dense buckthorn foliage. Due to the uniform reappearance of the plants throughout the area, it was felt that they did not seed in from the adjacent areas.

Table 2. Native vegetation which re-established in plots 1 and 2, Pipestone NM, 1986 (Nomenclature follows Barkley 1986).

Scientific Name	Common Name
Ambrosia artemisiifolia L.	Common ragweed
Ambrosia trifida L.	Giant ragweed
Helianthus maximilianii Schrad.	Maximilian sunflower
Helianthus rigidus (Cass.) Desf.	Stiff sunflower
Helianthus tuberosus L.	Jerusalem artichoke
Menispermum canadense L.	Moonseed
Osmorhiza longistylis (Torr.) DC	Anise root
Oxalis violacea L.	Violet wood sorrel
Phalaris arundinacea L.	Reed canary grass
Polygonatum biflorum (Walt.) Ell.	Solomon's seal
Smilacina racemosa (L.) Desf.	False spikenard
Smilacina stellata (L.) Desf.	Spikenard
Sporobolus heterolepis (A. Gray) A.	GrayPrairie dropseed
Thalictrum dasycarpum Fisch. & Ave-Lall.	Purple meadowrue
Tradescantia bracteata Small.	Spiderwort

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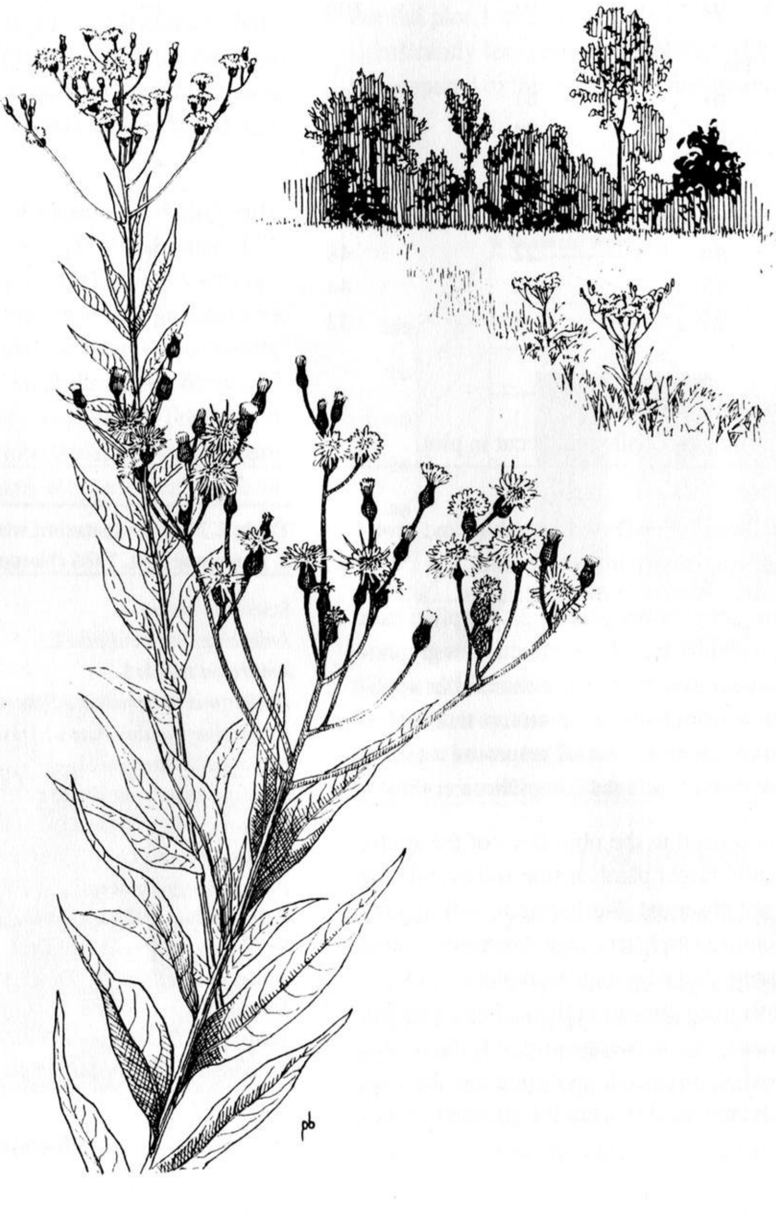

ABOVEGROUND BIOMASS IN TALLGRASS PRAIRIE: EFFECT OF TIME SINCE FIRE.

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Abstract. Previous research on the Konza Prairie Research Natural Area (KPRNA) has indicated that the interval between fires may influence the magnitude of biomass production responses to fire. To test this hypothesis, we estimated total aboveground biomass (grass+forbs+current year dead biomass) in burned watersheds that varied in fire history from 20 years of annual spring burning to fire exclusion for 18 years, and in an unburned watershed. In addition, we measured tiller density of big bluestem (*Andropogon gerardii*), the dominant grass of Konza Prairie. Tiller density was generally greater (19%) in annually burned sites, but biomass production was significantly higher in watersheds that had been protected from fire for >10 years (557 ±33 g/m^2) relative to annually burned sites (422 ±10 g/m^2). The increased production response to fire in sites previously unburned for several years was attributed to the maintenance of high forb biomass in the year of the fire coupled with a significant increase in graminoid biomass in relation to unburned sites.

INTRODUCTION

Drought and fire are known to exert direct control on patterns of net primary production in the tallgrass prairie (Collins and Wallace 1990). Over a 17-year period, peak aboveground biomass on the Konza Prairie Research Natural Area (KPRNA) has ranged from <200 g/m^2 to 700 g/m^2. Annually burned lowlands are usually the most productive sites while unburned uplands are usually the least productive (Abrams et al. 1986). During this 17-year period, aboveground total biomass in annually burned sites averaged 482 g/m^2 (SE=24) in the lowlands and 386 g/m^2 (SE=19) in uplands. In unburned sites, total biomass averaged 341 g/m^2 (SE=19) in lowlands and 349 g/m^2 (SE=23) in the uplands. In contrast, biomass of forbs was greater in unburned sites (Abrams et al. 1986).

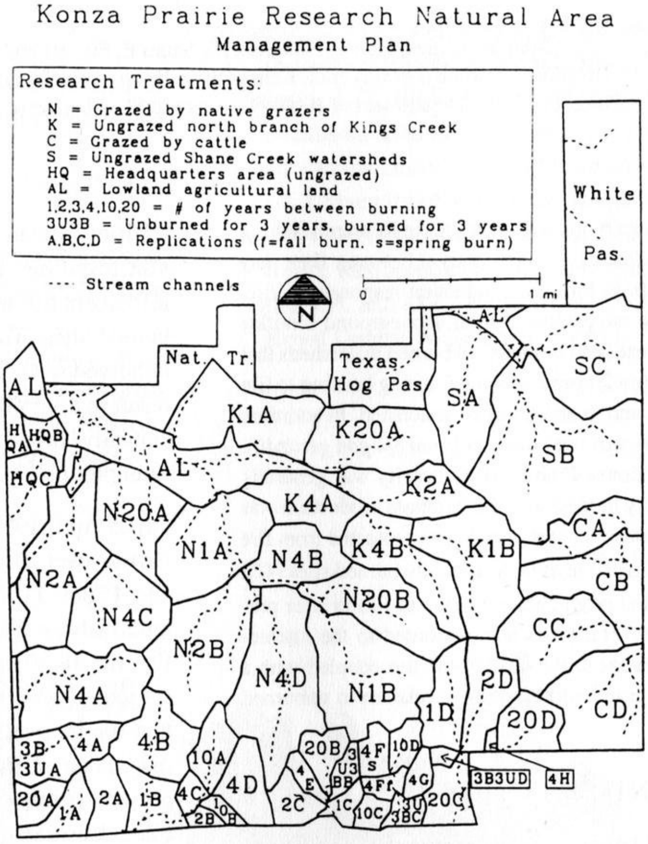
A variety of factors are influenced by fire that result in increased aboveground biomass in tallgrass prairie (Knapp and Seastedt 1986). Perhaps the most important function of a spring fire is the removal of old detrital biomass (Knapp and Seastedt 1986). This detrital layer reduces light available to emerging shoots, results in leaves developing "shade characteristics", keeps soil temperature cool in the spring, and, as a consequence, production on unburned sites is less than on burned sites. Many studies on KPRNA have documented this fire induced increases in aboveground biomass (Abrams et al. 1986, Briggs et al. 1989, Hulbert 1988, Knapp and Seastedt 1986, Seastedt 1985, Seastedt et al. 1991). In addition, Seastedt et al. (1991) reported that post-fire production responses to fertilizer (N) in sites with a history of infrequent fire was reduced relative to responses in annually burned sites. This suggests that N accumulates in soils of unburned sites. Thus, fire in an infrequently burned site will result in a significantly greater biomass response, relative to annually burned sites, because neither nitrogen or energy will limit production.

On 05 April 1991, a wildfire (a prescribed fire that escaped) burned over 2160 ha (5335 acres) of KPRNA (62% of the site; Figure 1). This wildfire burned watersheds (catchment units) whose fire histories varied from those protected from fire for 18 years to those annually burned for >20 years (Figure 1). We used this wildfire to evaluate the hypothesis that the interval between fires (fire history) influences the magnitude of the production response to fire. Below, we present estimates of peak aboveground biomass and also, tiller densities of big bluestem (*Andropogon gerardii*; the dominant grass of KPRNA) from 17 watersheds included in this wildfire. In addition, we estimated peak aboveground biomass from one watershed that has been unburned since 1971.

METHODS

Konza Prairie Research Natural Area is representative of the Flint Hills, a dissected upland with chert-bearing limestone layers. The ridges are usually flat with shallow, rocky soils, whereas the larger and wider valleys have deep permeable soils. The steep-sided hills are characterized by exposed Permian limestone and shale strata that prevented cultivation. Elevation on KPRNA ranges from 320 m to 444 m, with most of the land in the range of 366 m to 427 m. This native tallgrass prairie is dominated by big bluestem, little bluestem (*A. scoparius*), and switch grass (*Panicum virgatum*; Freeman and Hulbert 1985).

An experimental plan initiated in 1971 (Hulbert 1973) placed different watersheds (catchment units) under a variety of prescribed spring burning (mid-April) regimes ranging from annual, 2-, 4-, and 10-year intervals to long-term unburned sites. (Figure 1). Most watersheds have either Florence cherty clay loam soils on the broad, nearly level uplands or lowland Tully silty clay loam soils sites (Jantz et al. 1975). While portions of the site have been grazed by cattle or bison, only



ANALYSIS OF 05 APRIL 1991 WILDFIRE

WATERSHED	LAST YEAR BURNED	YEARS SINCE LAST BURN
001C*	1990	1
001D*	1990	1
002C	1989	2
002D*	1990	1
004E*	1987	4
004F*	1989	2
004G	1988	3
004H	1990	1
010C*	1981	10
010D*	1986	5
020B*	1973, (75)	18
020C*	(72-77, 1980)	11
020D*	1980	11
033B*	1989	2
033C*	1989	2
033D	1990	1
N20A	1990	1
N20B*	1980	11
N01A	1990	1
N01B*	1990	1
N02B*	1990	1
N04B	1989	2
N04D*	1988	3
K20A	1980, (85)	11
K01B	1990	1
K02A	1990	1
K04A	1989	2
K04B	1988	3
C20A	1980, (83)	11
C01A	1990	1
C02A	1989	2
C02B	1990	1
S03A	1986	5
S03B	1990	1
S03C	1989	2

() Partial Burn

* = Aboveground biomass was estimated from this watershed

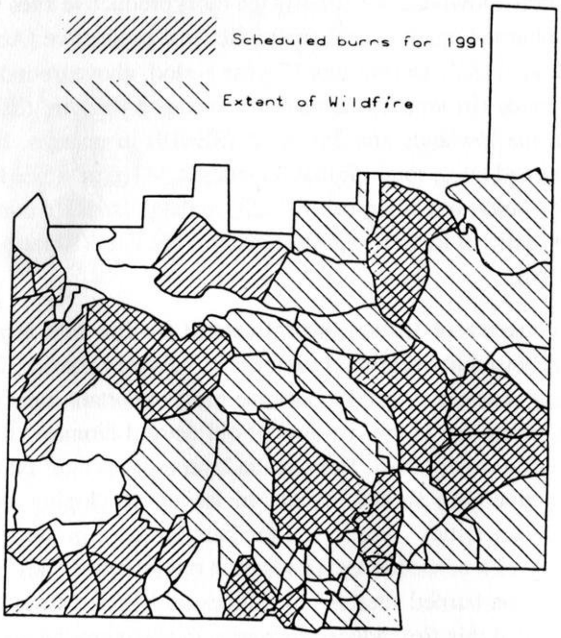


Figure 1. 1a. Konza Prairie Research Experimental Design showing fire intervals.
1b. The area burned on Konza Prairie by the wildfire of 05 April 1991.

Table 1. Peak mean (SE) aboveground biomass (g/m^2) on tallgrass prairie watersheds with different burn regimes. Values with the same letter are not significantly different at $P<0.05$ using Duncan's multiple range test.

YEARS SINCE LAST FIRE	TOTAL ABOVEGROUND BIOMASS (g/m^2)	GRASS (g/m^2)	Forbs (g/m^2)
1-2 (320)*	422 (10.3) C	359 (9.7) A	63 (4.0) C
3-5 (160)*	441 (15.4) CB	352 (13.4) A	116 (10.4) B
6-12 (160)*	493 (18.5) B	325 (16.7) A	141 (11.3) B
>12 (40)*	557 (33.3) A	310 (25.1) A	248 (29.4) A
Unburned (20)*	455 (30) B	226 (22.3) B	190 (30) B

* = number of 0.1 m^2 plots sampled

data obtained from watersheds ungrazed for at least 12 years are reported here.

To estimate peak aboveground biomass in 17 watersheds, 680 0.1 m^2 quadrats (20 per soil type from each watershed; soil type=Florence and Tully) were harvested in mid-August 1991 at sites with various burning histories (Figure 1). In addition, 20 0.1 m^2 quadrats were harvested from an unburned watershed (unburned for >20 years). This protocol is adequate to sample aboveground biomass and to detect the experimental effect of fire in this biome (Briggs and Knapp 1986). Detailed methodology for sampling the aboveground components are given in Abrams et al. (1986) but briefly, plant material was separated into graminoid and forb material (including a minor woody plant component), oven-dried at 60 C for 48 hr, and weighed to the nearest 0.1g.

Tiller density of big bluestem was measured on the uplands and lowlands of six watersheds that were burned during the wildfire in 1991. The watersheds included two burned annually for >10 years, two burned every four years, and two unburned for >10 years (Figure 1). Eighty random samples per fire history treatment were measured four times throughout the growing season.

For statistical analysis of aboveground biomass data, watersheds were grouped based upon past fire history. Groups were 1) watersheds burned annually or every 2-years for the past five years (N = 320 quadrats); 2) watersheds last burned 3-5 years before 1991 (N = 160 quadrats); 3) watersheds last burned 6-12 years before 1991 (N = 40 quadrats); 5) the unburned watershed (N=20 quadrats). These groups were selected based on results from Seastedt et al. (1991). ANOVA ($P<0.05$) on total, grass and forb biomass was conducted using PC-SAS (GLM Procedure, SAS, 1981). ANOVA with the least significant difference (LSD) method was used for pairwise comparison of tiller density data.

RESULTS AND DISCUSSION

On watersheds burned annually or biennially, total peak aboveground biomass was not significantly different from watersheds burned for the first time in 3-5 years (Table 1). However, on sites burned for the first time in 6-12 years, total peak aboveground biomass was significantly higher than watersheds burned at least biennially. The greatest biomass response was measured in watersheds burned for the first time in >12 years (Table 1). Peak grass biomass was not significantly different between fire history groups, but was significantly higher than in the unburned watershed. Forb biomass, however revealed a strong response to fire history (Table 1). A significant ($P<0.001$) difference in total, grass, and forb biomass was detected between upland and lowland soil types, thus a separate analysis was used for each soil type.

On upland sites, peak total aboveground biomass was not significantly different between watersheds burned at least biennially and watersheds burned for the first time in 3-5 years (Figure 2). On watersheds burned for the first time in 6-12 years, peak aboveground biomass was significantly higher than in watersheds burned at least biennially, but

Table 2. Big bluestem (*Andropogon geradii*) tiller densities per m^2 (mean and SE) from watersheds that differed in the years they were last burned. Values with the same letter are not significantly different at $P<0.05$ using LSD.

BURN HISTORY	MAY	JUNE	JULY	AUGUST
BURNED ANNUALLY	782 (32.5) A	1013 (30.5) A	1022 (29.4) A	989 (26.8) A
BURNED EVERY 4 YEARS	642 (29.9) B	972 (33.8) AB	964 (35.2) A	926 (25.1) AB
UNBURNED >10 YEARS	550 (31.7) C	906 (29.7) B	948 (30.9) A	866 (24.9) B

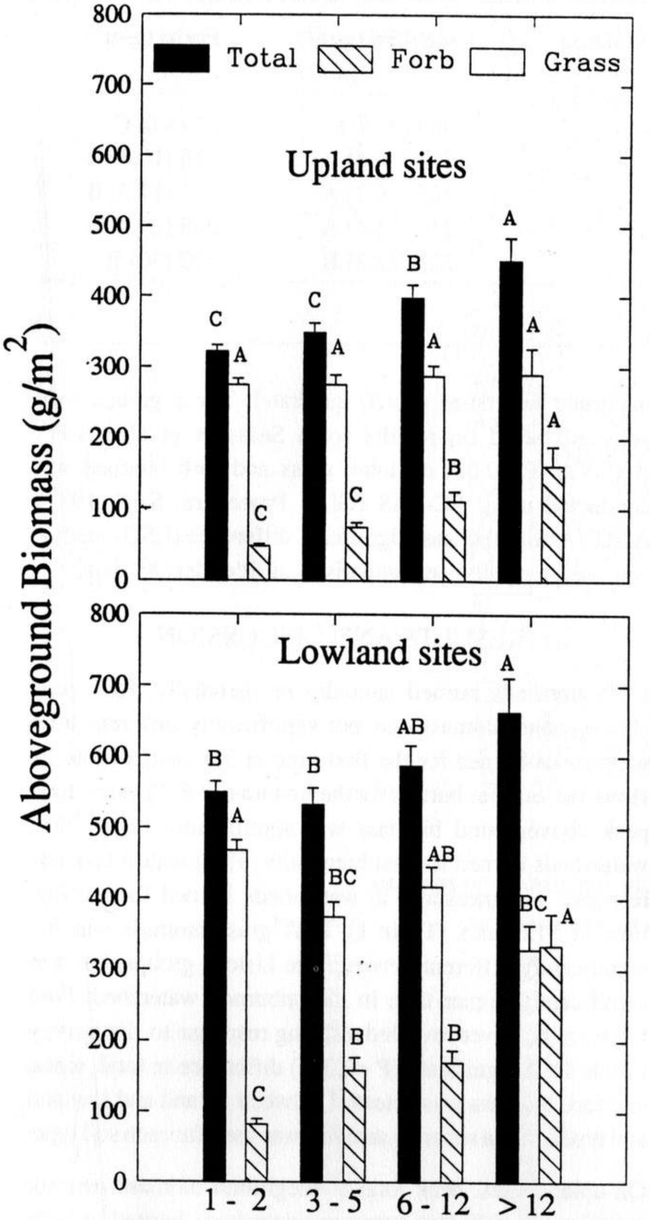


Figure 2. Peak above ground biomass (+SE of the mean) of watersheds on Konza Prairie Research Natural Area in 1991 differing in year since last burn. Bars with same letters are not significantly different at P<0.05.

lower than watersheds burned for the first time in 12 years. No significant difference between fire history groups was detected in grass biomass, but forb biomass was significantly higher on sites previously unburned for >6 years (Figure 2).

On lowland sites, biomass was greater than upland sites in all four groups, but the pattern of difference among groups was similar to upland sites in total aboveground biomass (Figure 2). However, peak grass biomass showed a negative response to time since last fire, as grass biomass decreased with increased time since last fire (Figure 2). Even so, grass biomass in watersheds unburned for >12 years was greater than in unburned sites. As in upland sites, forb biomass increased with increasing interval since last fire (Figure 2).

Tiller densities of big bluestem varied across the watersheds ranging from a low of 550 tillers per m^2 in May on watersheds unburned for >10 years to over 1012 tillers per m^2 on annually burned watersheds (Table 2). During all four measurement dates, densities of tillers were higher on annually burned watersheds compared to watersheds burned less frequently (Table 2). In previously unburned watersheds, tiller densities increased over the growing season, a pattern not seen in the annually burned sites.

Abrams et al. (1986) reported that biomass of gramminoids was 40% lower and forb biomass was 200-300% greater in unburned than in annually burned sites. Our data are consistent with this (Table 1). The lack of a significant difference in post-burn grass biomass between sites previously unburned vs. those annually burned in this study suggests that graminoids responded rapidly in these previously unburned sites, as did tiller density (Table 1). Moreover, the maintenance of high forb biomass after fire indicates that one year of fire is not sufficient to significantly decrease the importance of forbs in these communities. Thus, maximum levels of biomass in sites burned for the first time in several years can be attributed to the large graminoid response coupled with the presence of high forb biomass (Table 1, Figure 2). This is likely a nonsustainable phenomenon (Seastedt and Knapp 1993) since continued burning would reduce forb biomass and increase N limitations (Seastedt et al. 1991).

The 1991 wildfire may had different effects on the grassland vegetation compared to a prescribed fire. Fire temperature during a spring burn is highly variable in tallgrass prairie with headfires usually hotter than backfires (Gibson et al. 1990). In addition, areas that have not been burned for many years may have hotter fires than areas burned annually. However, in an earlier study on Konza Prairie, maximum fire temperatures did not differ significantly between sites burned annually and sites burned for the first time in 15 years (Gibson et al. 1990). Bidwell et al. (1990) found that in an Oklahoma grassland, peak aboveground biomass of tallgrasses was greater on headfired plots (typical of our wildfire) than on backfired plots, while the opposite occurred for forb peak aboveground biomass. We believe that the responses we report are not due to the type of fire (wildfire as opposed to a prescribed burn), as the total aboveground biomass on the sites which had burned annually for >17 years had similar production values to years when they had been burned during prescribed fires (17 year mean 434 ±24 g/m^2 vs. 422 ±10 g/m^2 during this wildfire).

CONCLUSION

In conclusion, tallgrass prairies are subject to considerable spatial and temporal variation in factors influencing NPP (fire, drought, grazing, etc.). Previous studies have shown that infrequent fires may maximize species diversity of plants and insects (Gibson and Hulbert 1987, Evans 1984). Data from this study suggest that aboveground biomass may also be maximized under these conditions.

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THE BRECKSVILLE PRAIRIE RESTORATION: A QUANTITATIVE LOOK AT THE GROWTH OF PLANTED SPECIES

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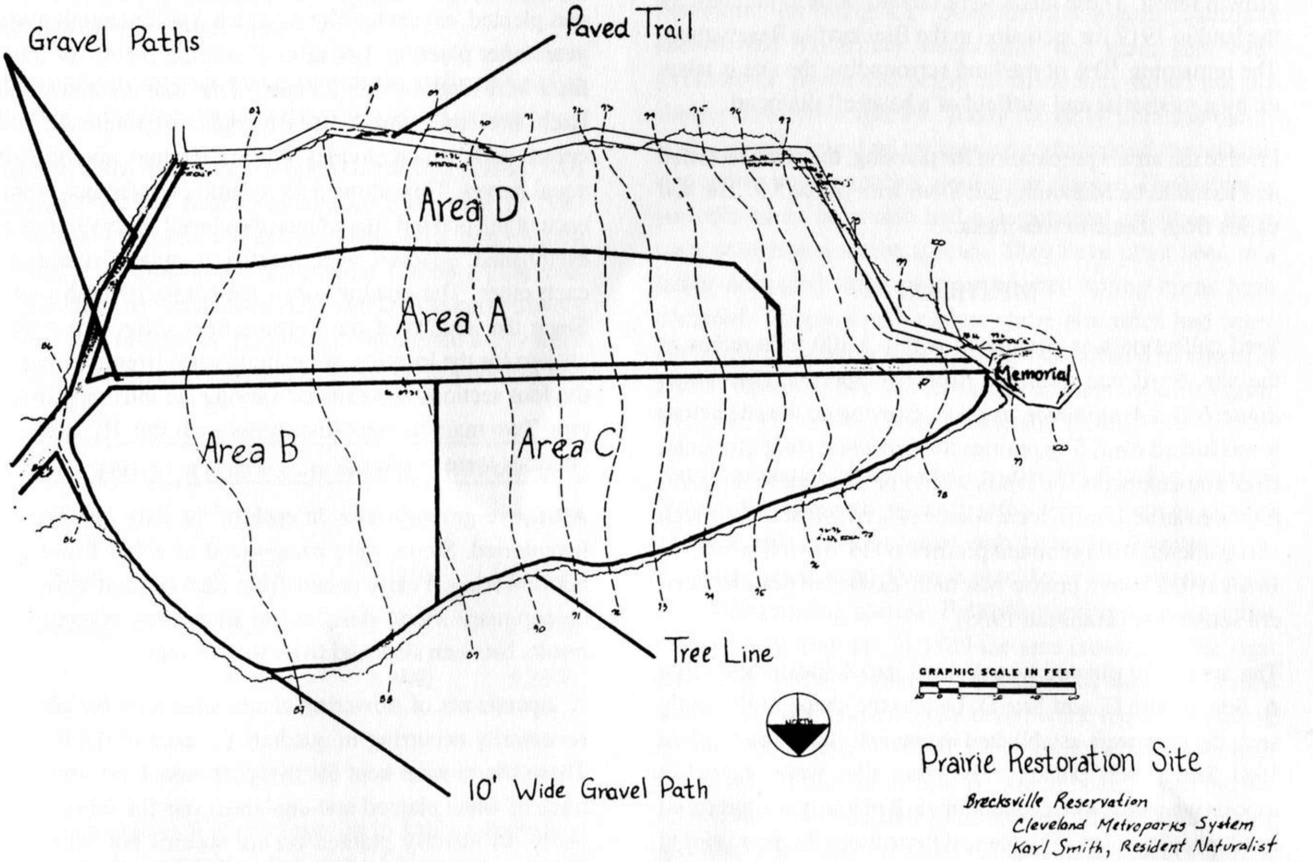
Abstract. From 1983 to 1991 a study was undertaken to monitor the growth on the prairie restoration at the Brecksville Reservation. Fifty square quadrats, one half meter on side, were randomly located along transects crossing the four sections of the restoration. These were inventoried during the summer growing season. The four sections were planted in successive years. The study has established the density, frequency, and percentage of planted prairie species each year. In 1991, for all 50 quadrats inventoried, the percentage of plant stems counted that were from planted prairie species, approached 93%. The density of prairie species varied as the planted species matured over the first few years of growth and with prescribed burning.

INTRODUCTION

Since the first planting of prairie species at the University of Wisconsin's arboretum to the many projects that followed this historic first effort, researchers and restorationists have reported on the success of native prairie plantings (Kirt 1992). One of the goals of the Brecksville Prairie Restoration was to quantitatively monitor the growth of planted species for an extended period of time. For the past ten years data on frequency, density, and percent of prairie plants has been collected. This data has been used to determine standards by which future prairie plantings can be assessed.



Map adaptations by Karen Scott

Figure 1. Prairie restoration site, Brecksville Reservation.

Table 1. Percentage of prairie plant stems rounded to nearest whole percent. Quadrats per site: A=10, B=12, C=16, D=12.

	1983	1984	1985	1986	1987	1988	1989	1990	1991
Site A	57%	64%	80%	83%	92%	94%	83%	81%	94%
Site B	43%	52%	90%	86%	98%	99%	92%	98%	99%
Site C		15%	57%	45%	76%	95%	92%	86%	90%
Site D			29%	33%	57%	69%	71%	78%	90%

Study Area

The Brecksville Prairie Restoration is a 0.8 hectare site located to the east of the intersection of state routes 82 and 21 in Brecksville, Ohio. The land is part of the Brecksville Reservation, a unit of the Cleveland Metroparks. The site chosen was formerly an old field which contained several species associated with prairies including tall goldenrod (*Solidago altissima*), black-eyed susan (*Rudbeckia hirta*), fringed loosetrife (*Lysimachia ciliata*), New England aster (*Aster novae-angliae*), and foxglove beardtongue (*Penstemon digitalis*) (Weaver 1954, Cusick-Troutman 1978). Approximately 90% of the study area is surrounded by second growth forest. These lands were farmed prior to purchase of the land in 1917 for inclusion in the Brecksville Reservation. The remaining 10% of the land surrounding the site is taken up by a memorial and outfield of a baseball diamond.

Prior to the area's preparation for planting, the soil was tested and found to be Mahoning silt loam with pH of 5.9. The soil varies from mesic to wet-mesic.

METHODS

Seed collection was completed within a 100 mile radius of the site. Seed was gathered from two species, *Penstemon digitalis* and *Aster novae-angliae*, growing on the site before it was turned over. Slip prairies located along steep creek and river embankments, on lands within or adjacent to the park, provided an additional local source of seed. Most seed though was gathered from remnant prairies 60 to 100 miles west of Brecksville, where prairie was more extensive prior to modern settlement (Transeau 1935).

The area to be planted was divided into 4 sites labeled Site A, Site B, Site C, and Site D. Due to the shape of the study area, the sites were established in unequal sizes (see map). In 1981 Site A was planted. The other sites were planted in successive years. The ground for each planting was prepared in advance by rotovating the soil three times the year prior to the planting. A tine harrow was used to smooth the soil in the year the planting took place. With the tines down a slightly grooved surface was left on the soil. Seeds were sown by hand and covered by dragging the tine harrow over them with the tines up. A landscape roller was then used to press down the soil to allow good seed contact with it (Smith and Stanley 1983). Big bluestem (*Andropogon gerardi*) was selected to be the dominant species and was planted with greatest frequency, except on the low wet end, where prairie cordgrass (*Spartina pectinata*) was planted in greatest abundance. The seed mixture for forbs increased in number of species planted, but not in volume, after the first planting (Table 4) (Smith personal communications).

The on-going monitoring of the restoration was begun in 1983. Transects and quadrats were established the year after planting on each site. Monitoring began the year after a site was planted, except for Site A, which was first monitored two years after planting. Location of starting points for transect lines were randomly set for each of the four planted sections. Each site has transect lines marked perpendicular to the center path which divides the prairie into approximately equal halves. This allowed for a common reference point for each of the planted areas. Once the eleven transect lines were established, quadrats were located at equal distances from each other. The quadrats span the length of each transect. Since the lengths of the transect lines differ, the intervals chosen for the location of quadrats vary. Irregular shapes of the four sections necessitated varying the intervals for quadrats. Two main transect lines cross each site. By 1985 all 50 quadrats were in place.

All above ground stems in each of the fifty quadrats were inventoried. Stems were categorized as either flowering or nonflowering. Yearly results from each quadrat were placed on summary sheets designed to allow easy comparison of results between sites and from year to year.

A separate set of flowering charts were kept for plants not necessarily occurring in quadrats for each of the four sites. These charts were kept for two purposes. First was to keep track of when planted and unplanted species flowered. Secondly, to identify planted prairie species not occurring in quadrats (Table 4).

Density has been computed for both individual prairie species and for all prairie species on a site. To compute density for each transect line, the number of occurrences of a species

Table 2. Density of prairie plant stems rounded to the nearest whole number (plants/.25 square meter). Quadrats per site: A=10, B=12, C=16, D=12.

	1983	1984	1985	1986	1987	1988	1989	1990	1991
Site A	30	48	79	92	42	77	73	109	29
Site B	25	109	132	140	66	132	162	140	73
Site C		36	47	97	56	81	90	77	62
Site D			19	50	45	101	110	102	65

was divided by the number of quadrats on that line. To find transect density, all prairie stem occurrences along a transect line were added together and divided by the number of quadrats. Density for a site was obtained by adding the total plants along all transect lines and dividing by the total number of quadrats.

Frequency was determined by how many quadrats a particular species occurred in along a transect line.

Percent of prairie plants was computed for transect lines and by site. The total of planted prairie species was divided by the total of all plants occurring.

Density and percent of prairie plants for the entire restoration were obtained by totalling the data from all 50 quadrats.

Prescribed burns on different sections of the four planted sites were begun in 1983 weather conditions permitting. In 1987 a formal burn plan was adopted that included a burn rotation for different sections of the restoration. The burn plan rotation called for one half of Sites A, B, and D to be burned every year, one half of Sites A, B, and C to be burned every three years, and one half of Sites B and C to act as a control and not be burned.

Table 3. The percent of prairie plant stems for all 50 quadrats.

	1986	1989	1991
Big Bluestem	87.22%	93.11%	92.76%
Other Grasses	6.22%	2.95%	2.48%
Forbs	6.56%	3.94%	4.76%

RESULTS

The high percentage of planted species in Table 1 appears to indicate that the restoration has met with success through 1991. Based on these percents a quantitative standard for evaluating the success of restoration plantings was determined to be 85% or greater after the sixth year of growth. A standard was also determined for average density and frequency of prairie grasses. After the sixth year of growth for individual quadrats, average density was set at 15 stems or greater and frequency at 70% or greater (Smith and Dvorak 1989).

During the first few years after each planting many early season weedy species were dominant. Kentucky bluegrass (*Poa pratensis*) and English plantain (*Plantago lancelota*) constituted more than 50% of the stems. After three years of growth on each site the tallgrass prairie plants began to dominate. The dense tall growth of plants such as big bluestem, Indian grass (*Sorghastrum nutans*), autumn sneezeweed (*Helenium autumnale*), and giant sunflower (*Helianthus giganteus*) began to shade and crowd out the shorter non-native species. Today the early Eurasian dominants are only found on the mowed paths around the restoration where prairie species were never planted. Undoubtedly periodic burns have also had a detrimental affect on these early season non-native species. They have often been in a rather advanced stage of growth when spring burns have occurred. Tallgrass prairie plants have also often had vegetative growth at the time of burning, but suffered no apparent losses. Research has shown that prairie plants will regrow after burns the same season (Anderson 1990).

Densities increased on each site after the first few years of growth. Big bluestem, with a frequency every year on all sites of 100%, was also the species with the highest density value. Densities began to go down as plant litter accumulated at the end of the growing seasons. Following spring burns densities immediately went up. In 1989 the area crossed by the west transect of Site A was burned. The quadrats along the burned western transect had a density of 89, while the density along the unburned transect was 57. Plant litter was very visible in the unburned section of Site A, which hadn't been burned since 1986. Accumulated litter covering the ground visibly had suppressed growth along the eastern transect of Site A. The area crossed by both transects of Site A was burned in 1990. Density of prairie plant stems increased dramatically from 73 in 1989 to 109 in 1990 (Table 2). Similar density patterns following burns have been exhibited on the other sites as well. In 1986 Site B was burned and had a density for prairie plant stems of 140. In 1987 it was not burned and density fell to 66 on the site.

Big bluestem became established as the main species of this mesic to wet-mesic restoration (Table 3). The two other grasses that occurred in quadrats over the years are Indian grass and switch grass (*Panicum virgatum*). As the plants matured on the restoration, the relative abundance of grasses and forbs leveled off (Table 3). The percentage of grasses to forbs compared favorably with Weaver's classic studies of big bluestem dominated lowland communities (Weaver 1968). In his sample of 155 quadrats on naturally occurring tallgrass prairies, forbs constituted 3.60% of plant cover.

Table 4. Species planted by site; Frequency from 1991; Location on prairie (Edge - the outer 150 cm from a prairie border, Interior - inside of 150 cm); and * = No visible germination.

Grasses	Sites	Frequency	Edge	Interior
Andropogon gerardi	ABCD	100%		x
Andropogon scoparius	ABCD	0	x	
Elymus canadensis	CD	0		x
Panicum virgatum	ABCD	2%		x
Sorghastrum nutans	ABCD	18%		x
Spartina pectinata	AB	0		x
Forbs				
Allium cernuum	ABCD	0	x	
Anenome virginiana	ABCD	0	x	
Asclepias hirtella	ABCD	*	x	
Asclepias incarnata	CD	0	x	
Asclepias sullivantii	ABCD	0		x
Asclepias tuberosa	ABCD	0	x	
Asclepias verticillata	CD	0	x	
Asclepias viridiflora	ABCD	0	x	
Aster novae-angliae	ABCD	0		x
Baptisia leucantha	D	0		x
Cassia fasciculata	ABCD	0	x	
Cicuta maculata	CD	0		x
Cirsium discolor	ABCD	0	x	
Cirsium muticum	ABCD	0	x	
Coreopsis tripteris	ABCD	14%		x
Cypripedium candidum	AB	0	x	
Desmodium canadense	CD	0		x
Eupatorium altissimum	ABCD	6%		x
Euphorbia corollata	D	*		
Gentiana crinita	C	*		
Gerardia tenuifolia	D	*		
Guara biennis	CD	0		x
Helenium autumnale	ABCD	14%		x
Helianthus giganteus	ABCD	0		x
Helianthus mollis	CD	0		x
Heliopsis helianthoides	ABCD	0	x	
Hypoxis hirsuta	ABCD	0		x
Iris shrevei	D	0	x	
Latuca canadensis	ABCD	*		
Lespedeza capitata	C	0	x	
Liatris novae-angliae	ABCD	0	x	
Liatris spicata	ABCD	6%		x
Lilium michiganense	D	0	x	
Lobelia spicata	D	0	x	
Lycopus americanus	CD	0	x	
Lysimachia quadriflora	CD	0		x
Lythrum alatum	D	0		x
Monarda fistulosa	ABCD	4%		x
Onosmodium hispidissimum	ABCD	*		
Oxypolis rigidior	D	*		
Penstemon digitalis	ABCD	30%		x
Polygala senega	C	*		
Polygonatum canaliculatum	ABCD	*		
Prenanthes racemosa	ABC	0		x
Psoralea onobrychis	D	*		
Pycnanthemum virginianum	ABCD	6%		x
Ratibida pinnata	ABCD	0	x	
Rudbeckia hirta	ABCD	0	x	
Silphium terebinthinaceum	ABCD	4%		x
Silphium trifoliatum	ABCD	0	x	
Smilacina stellata	CD	0		x
Solidago ohioensis	ABCD	0	x	
Solidago riddellii	ABCD	0		x
Solidago rigida	ABCD	0	x	
Thalictrum dasycarpum	ABCD	0	x	
Tradescantia ohioensis	ACD	0		x
Viola sagittata	C	*		
Zizia aurea	D	0		x

DISCUSSION

Plants that registered a frequency in more than one year and are noticeably visible throughout the restoration, (Table 4), are nearing the "Long-term Adjustment Stage" for this restoration (Schramm 1992). Site D, being the most recent planting, appears to be in Schramm's third of the four stages, the "Closeout Stage". Both black-eyed susan (*Rudbekia hirta*) and grey-headed coneflower (*Ratibida pinnata*) appeared in quadrats the first few years of the inventory, but have now moved to the edge (occurring only within 150 centimeters from a border) of the restoration. Biennial guara (*Guara biennis*) has appeared in quadrats more than one year, but not every year. As a biennial, it moves around the sites. Sullivant's milkweed (*Asclepias sullivantii*) has been very visibly increasing, but has yet to appear in quadrats. Giant sunflower (*Helianthus giganteus*) and hairy sunflower (*H. mollis*) are also increasing visibly and have occurred in quadrats some years. Smooth white lettuce (*Prenanthes racemosa*) was once widespread on the restoration. Heavy grazing by white-tailed deer has probably eliminated the species from the prairie. Grazing by groundhogs, meadow voles and others has noticeably reduced populations of some plants. Site B, 99% big bluestem, has been intentionally grazed by horses to try to open it up for forbs (Smith 1992).

As densities of prairie plant stems increased, the percentage of unplanted prairie species stems tended to decrease. When Site A reached a density of 79 in 1985, only 20% of the stems counted were from unplanted species. A recognizable pattern for all four sites did not develop though. Site B had a density of 132 before 20% or less of the counted stems were from unplanted species. Sites C and D also varied in density number from Site A when percentage of unplanted stems went below 20%. But as with Sites A and B after the first few years of planting, densities of planted prairie species stems went up, as the percent of unplanted species stems went down. Once the restoration prairie was planted the most important ingredient was time, as Cottam (1987) found with the Curtis and Greene Prairies at the University of Wisconsin Arboretum. Adding prescribed burns as a variable did have the effect of increasing densities, but did not noticeably alter the time it took for the planted prairie species to reach a percentage of stems over 80% (Tables 1 and 2).

The careful soil preparation followed for all four sections of this restoration may have been a factor in the speed at which the prairie plants began growth and increased in density and frequency. Kline and Howell (1987) suggested that careful cultivation of an area to bare the soil prior to planting, rather than depending on a relay floristics model, allowed for faster prairie establishment.

CONCLUSIONS

The rich growth of the planted tallgrass prairie species has been the most important factor to date in the measured success of this restoration. With time, deep rooted, sod and clump forming prairie plants, have competed vigorously with non-prairie species once they have established themselves. Following prescribed burns densities have increased, but enough replications have not occurred to draw firm conclusions. The continuation of the quadrat study should help establish long term growth trends for the Brecksville Prairie Restoration and be of assistance to others monitoring reborn prairies.

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DEVELOPING A MANAGEMENT PLAN FOR ECOLOGICAL INTEGRITY FOR THE MILK RIVER NATURAL AREA AND KENNEDY COULEE ECOLOGICAL RESERVE, ALBERTA, CANADA

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Abstract. After two decades of study, evaluation and controversy, a management plan has been completed which provides the framework for conserving a representative example of the Mixed Grassland Natural Region in Alberta. This plan deviates from other government plans for protected areas in the direct involvement of local stakeholders in its development, implementation and monitoring. Implementation of the plan is based on a long-term monitoring program which is based on ecological principles. Flexibility and innovation are two of the key points used to try to maintain ecological integrity.

INTRODUCTION

The greatest loss of native grassland is through cultivation and other forms of development. In Canada, less than 24% of the mixed grassland, 27% of the northern fescue grassland and less than 1% of the tallgrass prairie are left in native state (World Wildlife Fund Canada 1989). Alberta has both mixed grassland and fescue grassland but lacks tallgrass. Canada does not have shortgrass prairie. Milk River Natural Area and Kennedy Coulee Ecological Reserve are publicly owned lands located in the extreme southeastern corner of Alberta in the Mixed Grassland Natural Region. These two sites are adjacent to each other (Figure 1) and together form an important conservation area with:

- wide diversity of habitats within a small area;
- the Milk River canyon, which is the deepest in the western Canadian plains;
- an igneous rock exposure -- one of seven in the grasslands of western Canada;
- extensive badlands with rare features such as crystalline boulders and concretions;
- archeological sites such as tipi rings, rock cairns and sites for vision quests;
- nesting sites for birds of prey such as prairie falcon (*Falco mexicanus*), golden eagle (*Aquila chrysaetos*) and ferruginous hawk (*Buteo regalis*);
- many plants that are rare or restricted in their distribution in Alberta and/or Canada;
- many animals that are rare or restricted in their distribution in Alberta and/or Canada;
- some of the most spectacular panoramic views in the Canadian plains; and
- a wildland character with vastness and a lack of man-made intrusions.

Because the two sites are beside each other, a management plan was developed to manage them as a single unit.

HISTORY OF THE SITE

There is a long history of ranching on the site since the turn of the century which is summarized in Brierley et al. (1989). By 1959, all of the area was included within the Lost River Ranch that had a total lease size of 58,308 ha (144,077 acres) (Breirley et al. 1989). In 1978 the size of the ranch was reduced by 40,470 ha (100,000 acres) to comply with the Public Lands Act. As a result, the Lost River Task Force was formed to make recommendations on the management of the ranch and of the lands removed from the ranch. One of the recommendations of the Task Force was that a portion of the former ranch lands form part of a protected area. These lands were removed from grazing and were placed under protective notation as a candidate ecological reserve. This was a result of lobbying for protection of the area since the 1970's.

In 1984, the ecological reserve proposal was presented to the public but it met with much controversy. There was considerable support for the proposal but many members of the local community, primarily hunters and ranchers, opposed it due to concerns they had with the size of the site and the restrictions that would be placed on traditional activities such as hunting and grazing. As a result, a task force of non-government stakeholders (Milk River Task Force) was formed to make recommendations on the status of the area and to provide general guidelines for management. The Task Force presented the government with its recommendations in 1987.

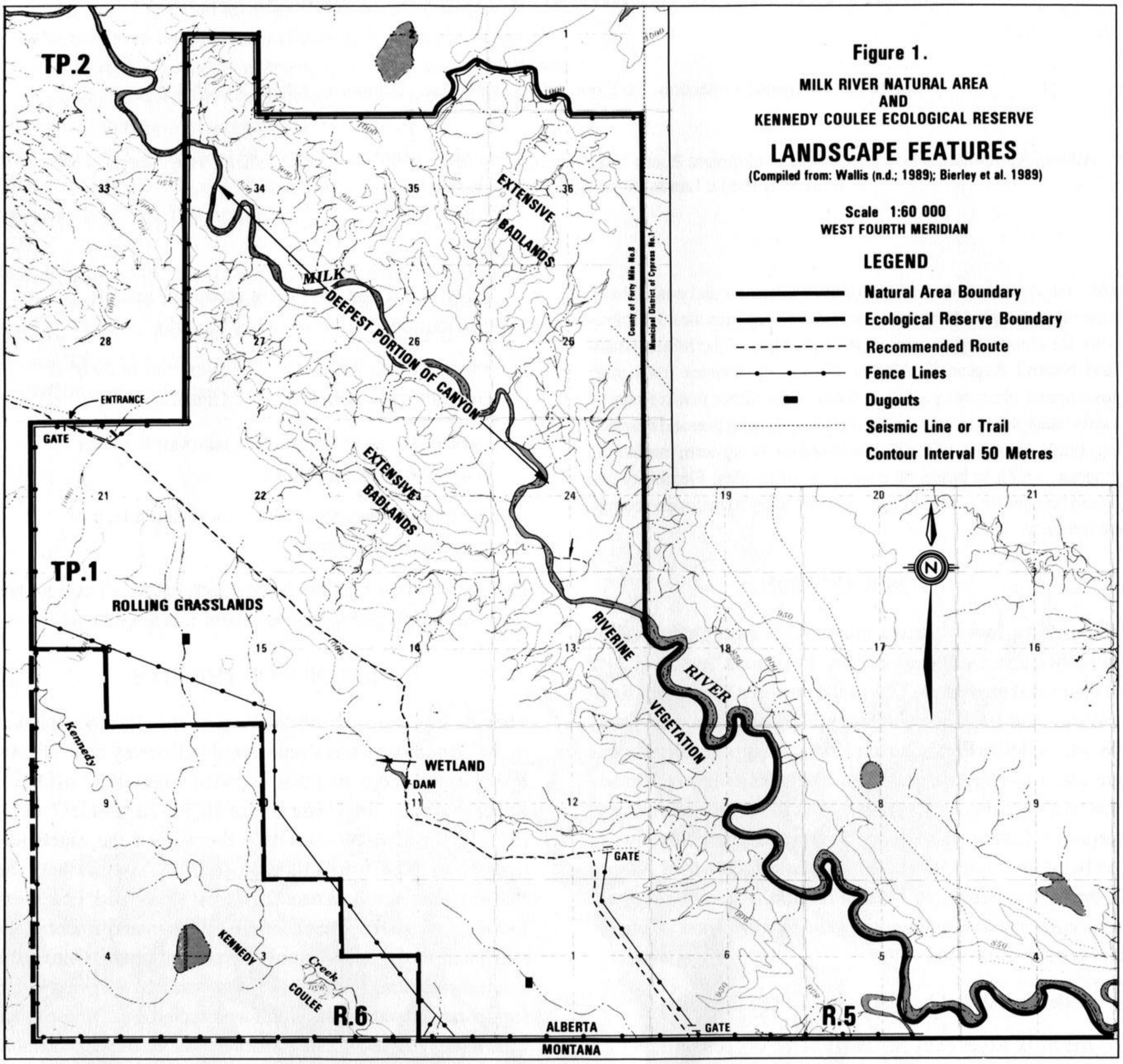


Figure 1. **Milk River Natural Area and Kennedy Coulee Ecological Reserve - landscape features.**

This lead to the establishment, through Order-in-Council, of Kennedy Coulee Ecological Reserve, which consists of 1,036 ha (2,556 acres), and the larger Milk River Natural Area, which consists of 5,344 ha (13,205 acres). (Although natural areas and ecological reserves are covered under the same legislation, the *Wilderness Areas, Ecological Reserves and Natural Areas Act*, there are significant differences between these two types of protected areas. Ecological reserves are highly protected while the legislation governing natural areas is much more flexible. For example, activities such as hunting are not allowed in ecological reserves but are in natural areas.)

DEVELOPMENT OF THE PLAN

The Task Force also recommended the formation of a management committee consisting of both government (5) and non-government (5) members and the local Member of the Legislative Assembly (ex officio). In 1990, the Milk River Management Committee held its first meeting. At this meeting they were presented with a draft of the management plan, encompassing both the ecological reserve and natural area, which had been drafted by the Public Lands Division of Alberta Forestry, Lands and Wildlife. The committee had to wrestle with some contentious issues, particularly fire and access within the area. It took more than a year of discussions to get a revised plan with which the committee felt comfortable. Development of a vision for the site by members was the first step in resolving these issues. Members were able to put aside personal biases and were able to discuss points and reach a consensus. As the local members of the committee provided input, representing the views of the community, throughout the development of the plan, it was favourably received by the public in 1991. The management plan has been finalized, approved and endorsed by the Ministers of Forestry, Lands and Wildlife and Tourism, Parks and Recreation.

The overall goal, or vision, for the site is "to protect and maintain the ecological and aesthetic character of a representative example of the Mixed Grassland Natural Region, with minimal human interference" (Hood and Gould 1992). Development of, and agreement on, the vision by members of the committee was an important first step as it ensured that everyone was working toward the same goal. This vision provided the framework around which the management decisions for both the ecological reserve and natural area were made.

The vision included three components:

1. to maintain ecological diversity, ecological processes, native species and habitats;
2. to protect rare and significant natural features and to maintain species and habitats; and
3. to ensure the availability of public land in a natural state for use by the public for recreation, education, scientific research or any other purposes, where compatible with the primary intent of protection.

IMPLEMENTATION OF THE PLAN

Given this vision for the site, the challenge lies in implementing the management plan. We started with an area that was relatively unaltered by man's intervention. Even though the site has a history of grazing by cattle, it had been well managed and is in good ecological condition.

Historically, large herbivores such as pronghorn (*Antilocapra americana*) and bison (*Bison bison*) were found in this area. Their grazing habits resulted in patchiness--some areas were heavily grazed, others ungrazed and still others received a moderate amount of use.

At Milk River, we have tried to develop a grazing strategy that provides some patchiness. We are using cattle to achieve this end while realizing that cattle do not mimic bison in their grazing patterns. Although bison will not be used on site in the near future due to concerns expressed by the local people, the opportunity to use them at some point is provided for in the plan. Under the grazing strategy that has been developed, Kennedy Coulee Ecological Reserve will not be grazed and serves as a core area, providing habitat for those species of both plants and animals, such as Baird's sparrow (*Ammodramus bairdii*) (designated as threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC)), that require taller grasses and a build up of litter.

Portions of the Milk River Natural Area will be grazed, providing a diversity of habitats for species associated with either taller or shorter grasses and various levels of litter. We expect areas of shorter grass around salt blocks and sources of water. Such areas will provide habitat for species such as Mountain Plover (*Charadrius montanus*) (designated as threatened by COSEWIC and endangered in Alberta).

Before putting cattle onto a portion of the site in 1991, a long-term monitoring program was initiated. This is the first such program for any protected area in Alberta. The management plan is strongly tied to the monitoring program as it will guide strategies for grazing. The ecological reserve, which is ungrazed, is serving as the control against which the effects of grazing are being measured. The results obtained from the monitoring program will be used to determine the need for grazing and on the effects of grazing on plant and animal communities and on rare species and their habitats. Should we find that the site is being affected adversely by our grazing strategy, we will alter our strategy using the information that we have obtained from the monitoring program.

At the present time, we are monitoring the following for any effects from grazing: vegetation, populations of four nationally and provincially rare plants [smooth boisduvalia (*Boisduvalia glabella*), small evening-primrose (*Oenothera andina*), California oat grass (*Danthonia californica*) and one-spike oat grass (*Danthonia unispicata*)], breeding birds, including Baird's sparrow, small mammals, northern leopard frog *(Rana pipiens)* (proposed for designation in Alberta as an endangered species), nesting birds of prey, such as golden eagle, ferruginous hawk (designated as threatened by COSEWIC and endangered in Alberta), merlin *(Falco columbarius)* and prairie falcon, and eastern short-horned lizard *(Phrynosoma douglassi brevirostre)*(designated as vulnerable by COSEWIC). The monitoring program is a cooperative one with assistance coming from Alberta Forestry, Lands and Wildlife, World Wildlife Fund Canada, consultants, academics and members of the public. We will be expanding the monitoring program to include other species and/or habitats and more detailed analyses of population biology and dynamics depending on the availability of funds.

One of the most hotly debated issues among management committee members was that of fire. Although all members understand the role of fire in the grassland ecosystem; however, the local community expressed concerns related to safety and potential for damage to adjacent properties. At their request, prescribed burning will not be done in the near future. However, the plan does not preclude prescribed burning at some point, under strict conditions and upon consultation with the local community. We are documenting the response of the grassland through the long-term monitoring program. Transects are being established in different habitats that are burned and in areas that are burned at different times of the year. This information will then be used in the development of a fire management plan for the site. For example, a small area within the natural area burned in September 1991 as a result of a wildfire. Four transects have been established here and we are collecting information on the vegetation along these transects.

In addition to helping with the monitoring program, members of the public are actively collecting additional information on the features and use of the site. Such information will be used to identify other priorities for monitoring and general management of the area. All data is being housed with the government where it is being put into a database for linkage to a geographic information system (GIS).

All information collected through the monitoring program will be used to guide management activities on the site. The management plan is not a static document. We were careful to ensure that the plan was tied directly to the monitoring program. In this way, we were able to provide the flexibility needed to manage the site based on ecological principles.

One of the keys to the success of the protection of the site is the innovation of the management committee. The non-government members of the Milk River Management Committee are a registered society (Milk River Management Society). The Society has been issued a twenty-one year recreational lease for the natural area for one dollar ($1.00). We pursued this arrangement because it ensures that the Committee has control over the management of the site. This was important as we did not want to be bound by the traditional grazing lease/permit arrangements that are the normal types of dispositions on public lands. The Society wanted to be able to dictate the conditions for grazing including entering into a long-term contract with a local rancher of their choice. The Society currently has a contract in place that is flexible enough that it allows the Society to alter the grazing strategy depending upon the results of the monitoring program. This is the first time that grazing has been used as a management tool in Alberta. It is also the first time that a grazing contract has been issued on public land.

One additional advantage of this type of arrangement is that all monies received by the Society from the contractor are put back into the management of the site. This ensures that the site management, including the monitoring program, can continue as it is not dependent upon government funding and the idiosyncrasies of the government budgeting process. With the typical grazing lease/permit arrangements on public lands, monies are put back into General Revenue of the Alberta government and may not be available for site management.

SUMMARY

The keys to planning for ecological integrity are innovation and flexibility. It is also important that an overall goal, or vision, for the area be developed. At Milk River, we are attempting to ensure that its ecological and aesthetic character are maintained. The monitoring program, which is based on ecological principles, is being used to guide all management activities. Flexibility has been written into the management plan and the grazing contract to ensure this. Innovation is being used to find solutions to management and funding problems.

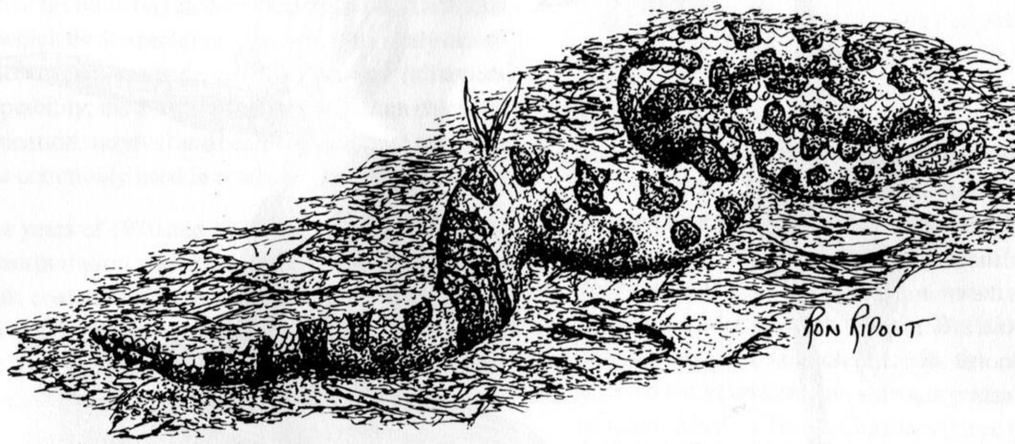
The long-term monitoring program at Milk River is the first for an ecological reserve or natural area in Alberta that is aimed at documenting the effect of management activities and at providing future management direction. This monitoring program is now serving as a model for management of other protected areas.

In summary, the success of any management planning exercise depends upon the commitment of the individuals. The Milk River Management Committee is successful because all members are committed to the long-term conservation of the site and are willing to try new, innovative ways of ensuring that protection.

ACKNOWLEDGEMENTS

We must recognize the efforts, specifically toward ensuring long-term protection for the area, that were taken by the predecessors of the Milk River Management Committee, i.e., members of the Milk River Task Force, interested agencies and members of the general public. We must also recognize the local ranchers whose management over the years has been instrumental in conserving the Milk River area as one of the best representatives of a native mixed grassland ecosystem in North America.

We would also like to thank D. Ealey, Editorial Services, Alberta Environmental Protection, W. J. Crins and A. Schwartz for reviewing and commenting on this paper.



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ROAD SALT EFFECTS ON THE GERMINATION OF EIGHT SELECT PRAIRIE SPECIES

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Abstract. Road salt (sodium chloride) as a de-icing agent has destructive effects on roadside vegetation (Dirr 1976, Hanes et al. 1976, Hughes et al. 1975, Westing 1969). This paper uses two greenhouse studies to explore the effects of sodium soil concentration on germination and seedling survival of prairie species. The species tested include buffalo grass (*Buchloe dactyloides* (Nutt.) Engelm.), sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.), Canada wildrye (*Elymus canadensis* L.), little bluestem (*Schizachrium scoparium* (Michx.) Nash), Indian grass (*Sorghastrum nutans* L.), roundheaded bushclover (*Lepedeza capitata* Michx.), purple prairie clover (*Dalea purpurea* Vent.), and greyheaded coneflower (*Ratibida pinnata* (Vent.) Barnhart). Sodium concentrations of 0, 500, 1000, 1500, and 2000 ppm for Experiment 1 and 0, 100, 200, 300, and 400 ppm for Experiment 2 were established in a sterilized silt loam soil mix. Germination, survival, stem height, foliage color and biomass data were collected from all species for a period of 8 to 16 weeks. Germination and growth were reduced in all species subjected to Na^+ concentrations greater or equal to 500 ppm. Of the species studied, buffalo grass demonstrated the greatest tolerance of sodium in terms of germination rate and biomass.

INTRODUCTION

The use of native plants along roadways has become a popular alternative to current roadway plantings throughout the Midwest (Harrington 1991). Several states, such as Iowa, Illinois, Minnesota, and Wisconsin, have experimented with native plants to create highly aesthetic, low maintenance ground covers. Accompanying these projects are specific environmental problems created by the unique often artificial habitats in which these species are planted. This study examines one facet of the roadside environment that influences species adaptability; the effects of road salt (sodium chloride) on the germination, survival and health of five grass and three forb species commonly used in roadside restorations.

Between the years of 1970 and 1979, the Wisconsin Department of Transportation undertook a study to determine the extent of salt contamination and accumulation in soils bordering its rural highway systems (Patenaude 1979). Both sodium and chloride concentrations had significant increases within 60 feet of the pavement and accumulated to a greater extent in fine rather than coarse grained soils. In sandy loam soils, sodium levels rarely exceeded 100 ppm while in the silt and clay loams of southeastern Wisconsin levels ranged from 100 to 400 ppm. In more metropolitan areas, such as Chicago, concentrations greater than 20,000 ppm have been found (Hughes et al. 1975, Dirr 1976).

Sodium chloride (NaCl) accumulation in plants affects ionic balances within the cell, as well as osmotic pressures, and normal cellular metabolism (Grueb et al. 1979, Menge and Kirkby 1978, Hanes et al. 1976, Westing 1969). Sodium can produce degrading effects on the soil's physical condition (Singer 1991, Mass 1986, Dorgan et al. 1982). At high concentrations, sodium (Na^+) readily bonds with the soil aggregates allowing clay and humus to disperse into individual hydrated particles instead of remaining flocculated. Soil permeability is decreased through reduced pore space. This impedes drainage, inhibits root penetration, and reduces plant growth.

This research addressed several questions including:

1) What is the relationship between sodium concentrations and the occurrence and timing of germination?

2) What is the relationship between sodium concentrations and height and color of seedlings during the period of the experiment?

3) What is the relationship between sodium concentrations and productivity as described by dried biomass of roots and shoots?

4) Which of the species tested is best suited for saline conditions?

METHODS

Selection of Species

The species were chosen as those commonly used in Wisconsin Department of Transportation roadside plantings, often selected for establishment ease and aesthetic value. Although seven species are native to Wisconsin, buffalo grass (*Buchloe dactyloides* (Nutt.) Engelm.) is a western U.S. species regarded as moderately salt tolerant. Buffalo grass was used to compare relative salt tolerance in the other species. The selected native species are: sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.), Canada wildrye (*Elymus canadensis* L.), little bluestem (*Schizachrium scoparium* (Michx.) Nash), Indian grass (*Sorghastrum nutans* (L.) Nash), roundheaded bushclover (*Lepedeza capitata* Michx.), purple prai-

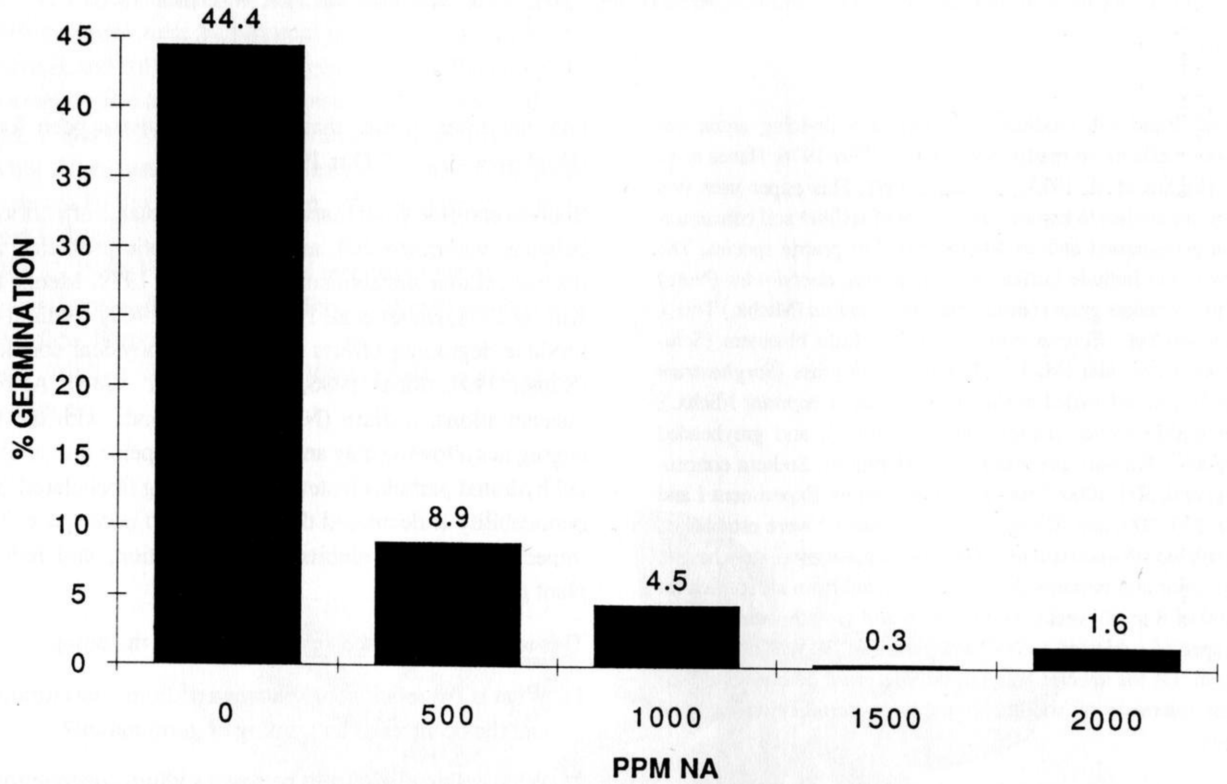


Figure 1. Cumulative germination rates for all species at Na$^+$ concentrations of 0, 500, 1000, 1500, and 2000 ppm.

rie clover (*Dalea purpurea* Vent.), and greyheaded coneflower (*Ratibida pinnata* (Vent.) Barnhart).

Experimental Design

Species were planted in six-inch plastic pots and represented by four replications of each Na$^+$ concentration within each study. Seeding density was at 5, 10, and 15 seeds per pot. Each species was planted at two of these densities to test for any influences of seeding density on germination. None was found. Densities used were based on recommendations by Rock (1977). The studies were set up as a randomized block design.

Silt loam soil was chosen as the planting substrate due to its ability to limit leaching of salts. The soil was sterilized for 1-1/2 hours at 108°C and 9.5 psi in an autoclave. Dispersion point was calculated at 690 ppm Na$^+$. This calculation, determined at the UW Soils Lab, is based on the soil's clay type, montmorillonite, and a 20% displacement of cation exchange capacity with Na$^+$ leading to dispersion. The amount of NaCl needed to raise the Na$^+$ in all pots to desired concentrations was calculated using the equation:

$$\text{mg NaCl to add/kg oven dry soil} = \frac{\text{ppm Na}^+\text{ desired}}{\text{kg oven dry soil/pot}}$$

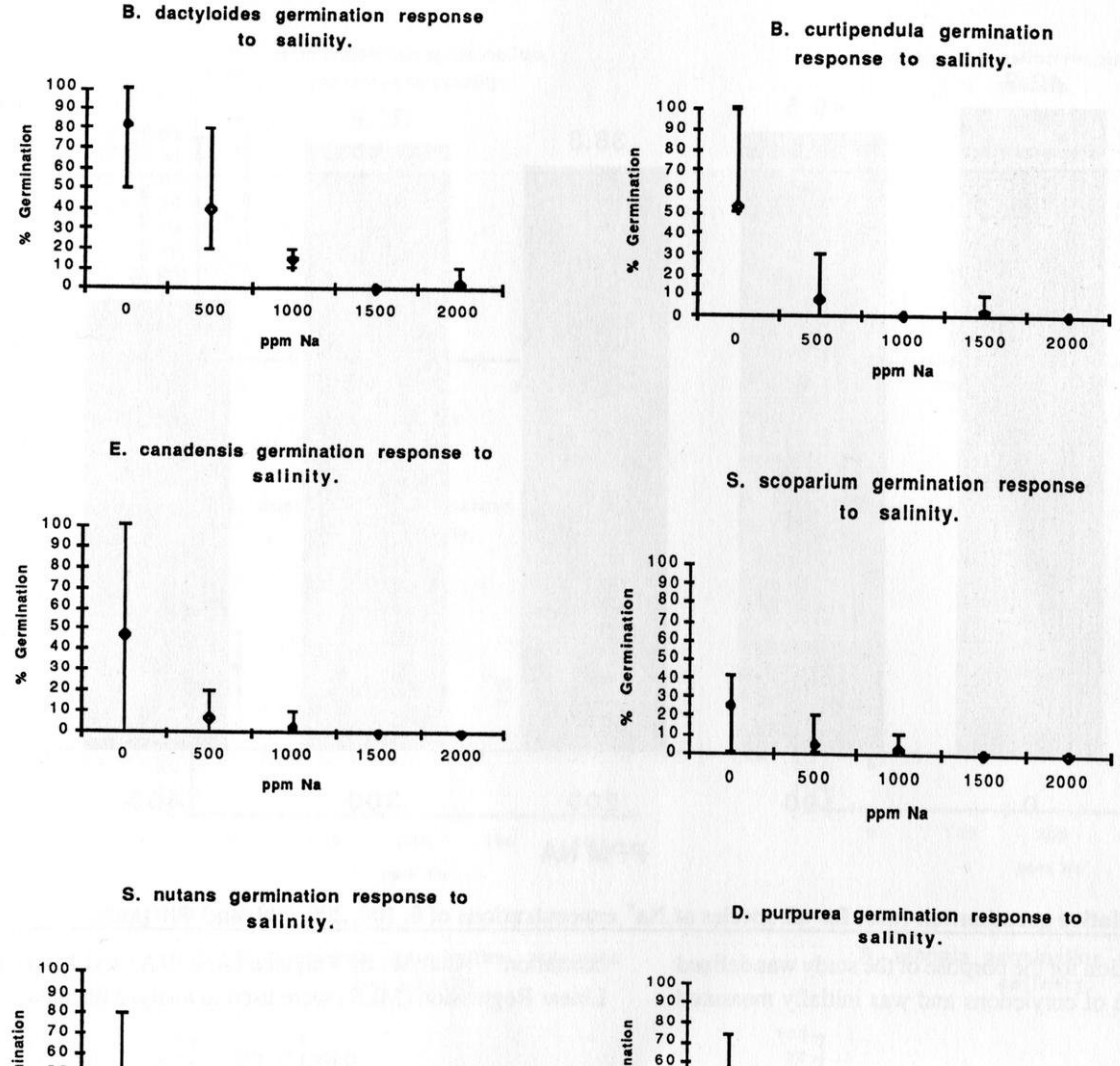
and added to distilled water for application.

Species were planted in soil with sodium concentrations of 0, 500, 1000, 1500, and 2000 ppm for the first study. Plants were grown for a total of eighteen weeks. The second study was conducted to test species at concentrations of 0, 100, 200, 300, and 400 ppm Na$^+$. These concentrations are typical of those found in a rural Wisconsin setting. This study lasted for a total of eight weeks. All soils at concentrations above 500 ppm Na$^+$ would be expected to experience dispersion.

Seed was dry stratified and all legumes inoculated with *Rhizobium* bacteria. 1500 grams of moist soil was added to each pot. The pots were lined with polyethylene bags intended to prevent leaching and promote germination. After seeding pot surfaces were gently packed, 50 milliliters of the appropriate salt solution was added and the top of the polyethylene bag was tied to prevent drying of the surface. The daily amount of water to be added was based on soil weight.

Data Collection

Measurements taken were for germination rate, survival, height, foliage color, biomass, and soil salinity. Soil samples were dried for 48 hours at 60° C in a forced-air oven and ground to a consistent grain size before tested using a YSI Model 31 Conductivity Bridge to determine salinity. Soil salinity was measured using the 1:1 soil:water method following *Recommended Chemical Soil Test Procedures*



B. dactyloides germination response to salinity.

B. curtipendula germination response to salinity.

E. canadensis germination response to salinity.

S. scoparium germination response to salinity.

S. nutans germination response to salinity.

D. purpurea germination response to salinity.

R. pinnata germination response to salinity.

L. capitata germination response to salinity.

Bars indicate high and low values for pots.

Figure 2. Germination rates of eight prairie species at Na$^+$ concentrations of 0, 500, 1000, 1500, and 2000 ppm.

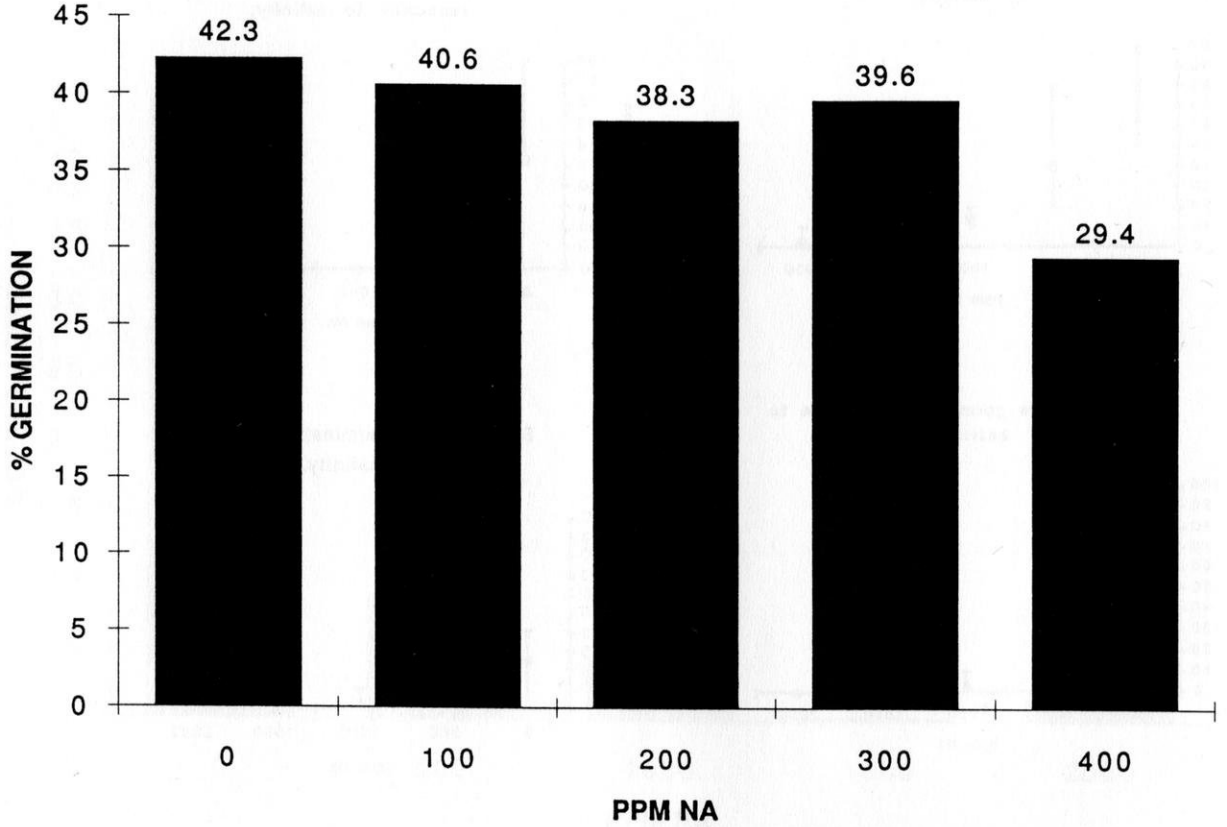


Figure 3. Cumulative germination rates for all species at Na$^+$ concentrations of 0, 100, 200, 300, and 400 ppm.

(1988). Germination for the purpose of the study was defined as the emergence of cotyledons and was initially measured on a daily basis.

Throughout the study, the number of plants per pot was noted on an every other day basis. Plant heights and colors were determined on a weekly basis. In order to prevent selection bias, five plants from each pot were chosen and measured to give a sample average. Leaf colors were visually matched to the color plates found in *Munsell Book of Colors* (1960). Biomass samples were collected at the conclusion of Experiment 2. Plant tissues were separated into roots and shoots, and dried for 48 hours in the forced-air oven at approximately 60° Celsius.

Germination rate and timing, percent survival of seedlings, and average height were analyzed according to two perspectives: a global or species-wide perspective and a species perspective. The global perspective evaluated all Na$^+$ concentrations on an experimental wide basis. Such an evaluation would ask a question such as "At what concentration does there appear to be a cumulative response by all species?" Species perspectives evaluated an individual species response to a Na$^+$ concentration and would ask for example, "How does this individual species respond to a given concentration?" Analysis of Variance (ANOVA) and Multiple Linear Regression (MLR) were used to analyze the data.

RESULTS

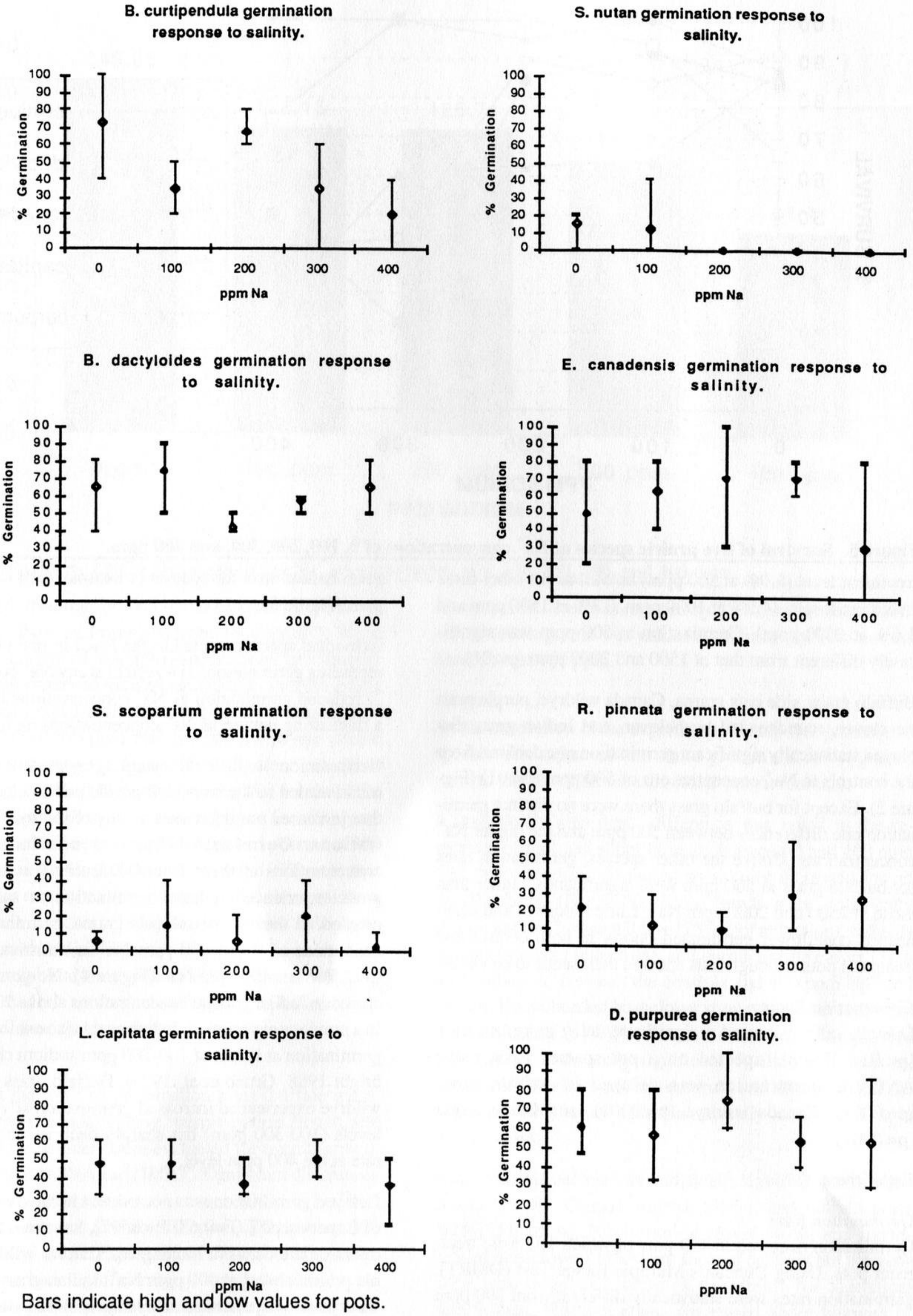
Experiment 1

Low germination limited the amount of analysis that was done. At the termination of the experiment, less than 1/4 of the pots had germinants. Of all measurements taken, only germination rate and timing data were judged to be sufficient for analysis.

Salinity levels within the pots reached concentrations placing them in non-saline (0 ppm), slightly saline (500 ppm), and moderately saline (1000 and 1500 ppm) and saline (2000 ppm) categories as defined in the handbook *Recommended Chemical Soil Test Procedures* (1988). In both studies salt concentrations were greatest within the top one inch of the soil profile and generally followed a decreasing gradient to the lower levels.

Germination Rate

Germination, when analyzed at a global perspective, was significantly reduced at Na$^+$ concentrations of 500 ppm ($p<.01$) (Figure 1). Contrasts in overall germination occurred between controls (44.4% at 0 ppm) and the lowest salt



Bars indicate high and low values for pots.

Figure 4. Germination rates of eight prairie species at Na^+ concentrations of 0, 100, 200, 300, and 400 ppm.

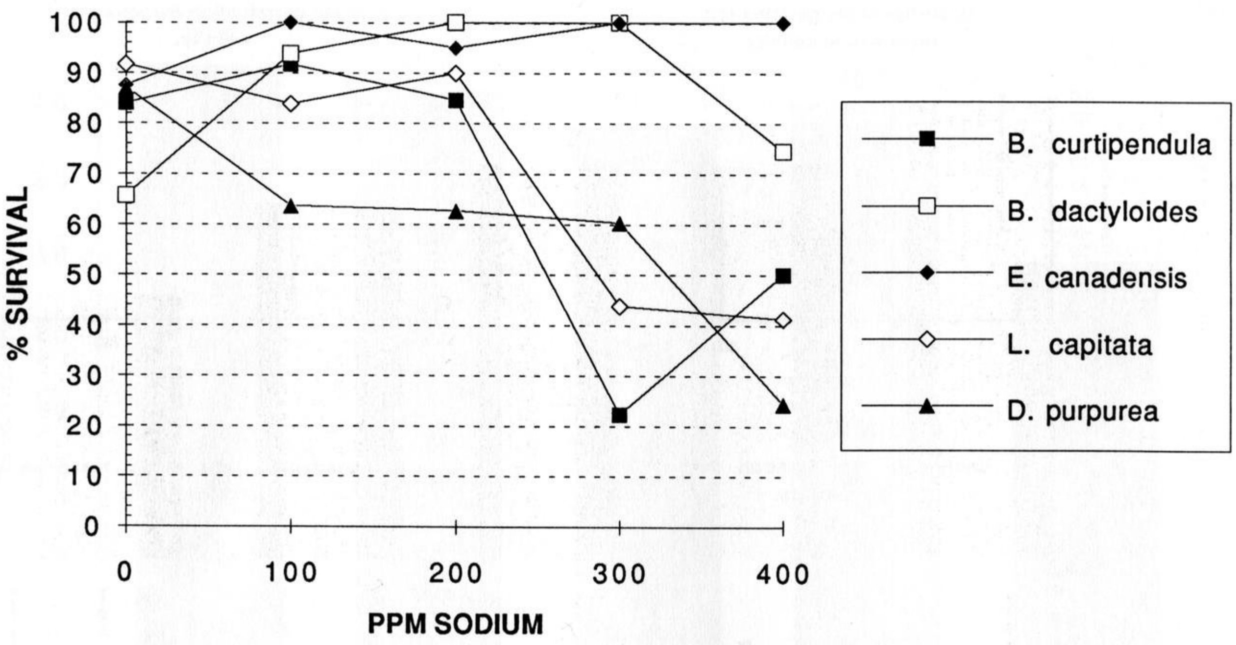


Figure 5. Survival of five prairie species at Na$^+$ concentrations of 0, 100, 200, 300, and 400 ppm.

treatment level (8.9% at 500 ppm) as well as the other three treatment levels; (4.5% at 1000 ppm, 0.3% at 1500 ppm and 1.6% at 2000 ppm). Germination at 500 ppm was significantly different from that at 1500 and 2000 ppm ($p<.01$).

Buffalo grass, side oats grama, Canada wildrye, purple prairie clover, roundheaded bushclover, and Indian grass displayed statistically significant germination rate declines from the controls to Na$^+$ concentrations of 500 ppm ($p<.01$) (Figure 2). Except for buffalo grass there were no distinct germination rate differences between 500 ppm and the higher Na$^+$ concentrations. Unlike the other species, germination rates for buffalo grass at 500 ppm were significantly higher than those at 1500 and 2000 ppm Na$^+$. Little bluestem and greyheaded coneflower germinated poorly in both control and treatment pots although tests showed their seeds to be viable.

Germination Timing

Overall, salinity caused a significant delay in germination ($p<.01$). When inspected on a per species basis using ANOVA, germination was delayed in buffalo grass ($p=.0004$), Canada wildrye ($p=.0001$), and Indian grass ($p=.0001$).

Experiment #2

Germination Rate

Germination occurred in 133 pots of which 102 were treatment pots. Using Duncan's Multiple Range Test (DMRT), germination rates were statistically different from 300 ppm to 400 ppm ($p<.05$). There were no significant differences in germination rates for species in treatments of 0 ppm to 300 ppm (Figure 3).

Individual species reacted to the NaCl in one of three ways regarding germination: 1) no effect at any Na$^+$ concentration; 2) reduced germination as Na$^+$ concentrations increased; 3) a fluctuating pattern as Na$^+$ concentrations increased.

Germination in little bluestem, greyheaded coneflower, roundheaded bushclover, and purple prairie clover was neither increased nor decreased by any of the soil Na$^+$ concentrations. Germination appears unaffected by Na$^+$ concentrations at these levels. Sideoats grama and Indian grass experienced reduced germination as salt levels increased. In the case of sideoats grama, germination at concentrations of 0 and 200 ppm Na$^+$ is statistically different ($p<.05$) from 400 ppm Na$^+$ (Figure 4). No germination occurred in Indian grass at concentrations above 200 ppm Na$^+$. In a previous experiment, Indian grass also exhibited reduced germination at levels of 100-200 ppm sodium chloride (Fulbright 1988, Grueb et al. 1979). Buffalo grass and Canada wildrye experienced increased germination at very low Na$^+$ levels (100-300 ppm) but sharply declined in germination rate at the 400 ppm level.

Delayed germination was not evident in the overall analysis of Experiment 2 ($F=0.68$, $P=.8517$), however, delayed germination did occur in Indiangrass, Canada wildrye and purple prairie clover at 400 ppm Na$^+$. Indian grass and Canada wildrye also experienced delayed germination in Experiment 1.

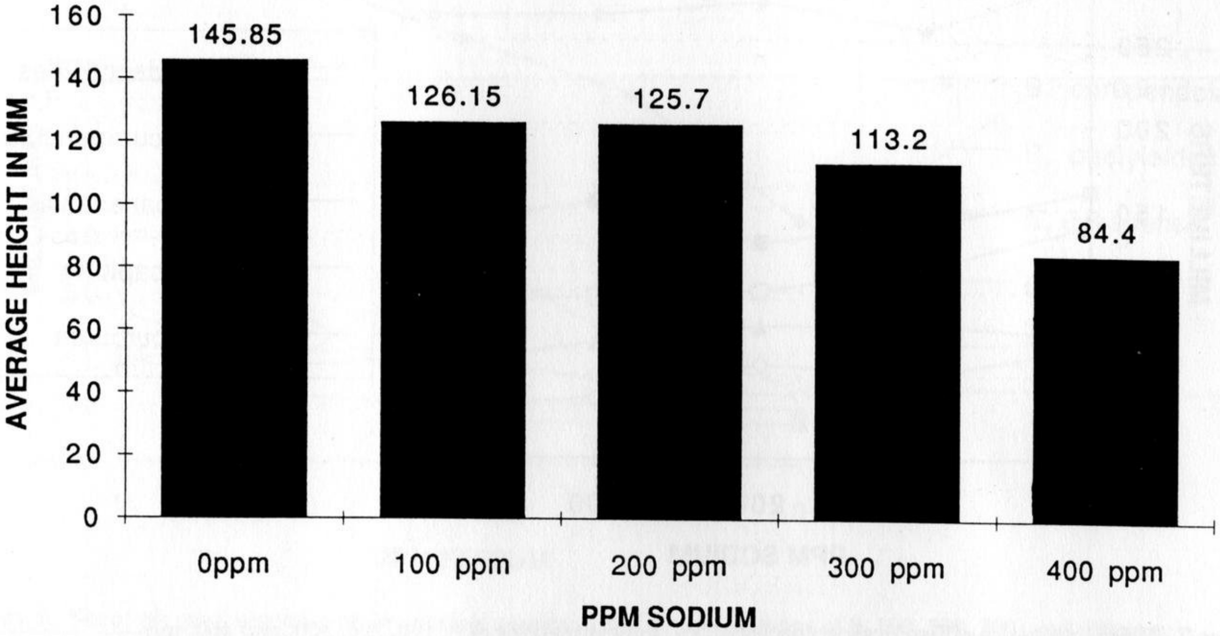


Figure 6: Cumulative height for all species at Na^+ concentrations of 0, 100, 200, 300, and 400 ppm.

Using DMRT, seedling survival was statistically different at 400 ppm Na^+ from all lower concentrations ($p<.01$). When considering survival of individual species after germination no trends were observed for Canada wildrye, little bluestem and greyheaded coneflower. Seedling survival was significantly reduced at 400 ppm Na^+ ($p<.05$) for purple prairie clover, and roundheaded bushclover (Figure 5). Buffalo grass seedlings had their highest survival at Na^+ levels of 200 ppm and 300 ppm and their poorest at 0 ppm and 400 ppm. Sideoats grama survived best at 100 ppm and poorest at 300 ppm and above. Levitt (1980) and Waisel (1972) note that several species require sodium as an essential element in low amounts while Larcher (1983) found several halophytic grasses to absorb sodium into the roots in order to increase osmotic potential and thus, potential for water absorption. Indian grass had no survival at 400 ppm. No foliage color changes were visually identified.

Height

Species with the top five germination rates (buffalo grass, sideoats grama, Canada wildrye, purple prairie clover, and roundheaded bushclover) were evaluated for overall growth of shoots using ANOVA and DMRT. Significant differences ($p<.05$) in total growth occurred between 400 ppm Na^+ and all other concentrations (control, 100 ppm, 200 ppm and 300 ppm) on a global scale (Figure 6). At the end of six weeks, salinity levels had significantly affected the heights of sideoats grama, purple prairie clover, and roundheaded bushclover (Figure 7). Purple prairie clover was reduced by 23% in height between controls and 400 ppm Na^+ and roundheaded bushclover was reduced by 55% over the same interval. Sideoats grama was reduce 32% in height between the controls and 400 ppm.

Biomass

At the conclusion of the experiment, the top five germinated species were separated into above ground and below ground parts to test for differences in dried weight biomass.

A statistically significant difference was noted in the responses of root and shoot biomass between 0 and 400 ppm Na^+. Root biomass decreased as salinity increased for all species tested (Figure 8). These trends were statistically significant for Canada wildrye (75% root reduction), sideoats grama (44% root reduction), and purple prairie clover (31% root reduction) between the controls and 400 ppm Na^+ and greater. Roundheaded bushclover showed obvious reduction in root biomass (64%), however, due to a small sample size this was not statistically significant. Buffalo grass was reduced only 8% between the controls and 400 ppm and the plants growing at 100 ppm Na^+ actually increased 22% in root biomass.

Shoot biomass decline was statistically significant in sideoats grama (55 %), Canada wildrye (49%), and buffalo grass (47%) (Figure 9). Purple prairie clover (46%) and roundheaded bushclover (34%) both showed declines but the variance was large and samples too small for statistical significance. Sideoats grama (increased shoot biomass of 60% between 0 ppm and 100 ppm Na^+) and buffalo grass (increased shoot biomass of 44% between 0 ppm and 200

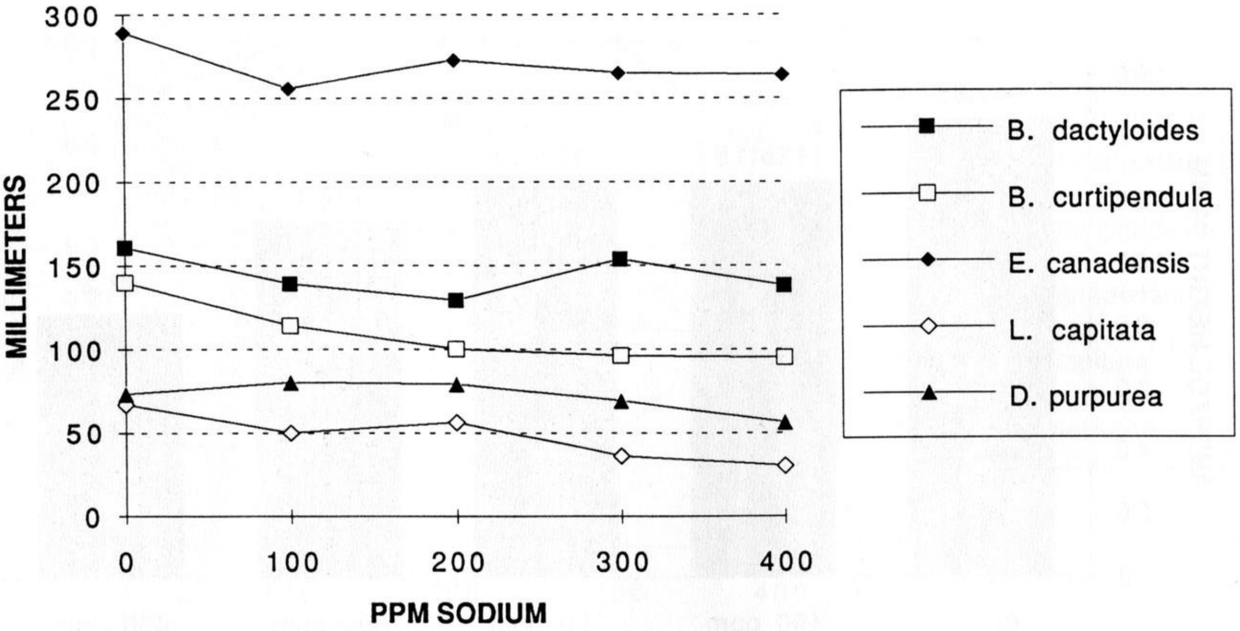


Figure 7. Height response of five prairie species at Na$^+$ concentrations of 0, 100, 200, 300, and 400 ppm.

ppm Na$^+$) showed stimulated shoot production at low salt levels.

CONCLUSIONS

Slightly saline conditions appear to affect the germination and early survival of prairie grasses and forbs. Germination, survival, overall height, and biomass each declined in all species at 500 ppm Na$^+$ and for some species at 400 ppm. Some species such as buffalo grass and sideoats grama appear to respond with increased germination and seedling survival at low salt levels of 100-200 ppm. This response may reflect the ability of some species to tolerate or utilize assimilated salts to their advantage. Although many species did not show statistically significant declines in germination rates at 400 ppm they did show germination delays. Indian grass, Canada wildrye and purple prairie clover each experienced delayed germination at Na$^+$ concentrations of 400 ppm and greater.

Once germinated many seedlings persisted although growth was slow and productivity as defined by biomass was re-

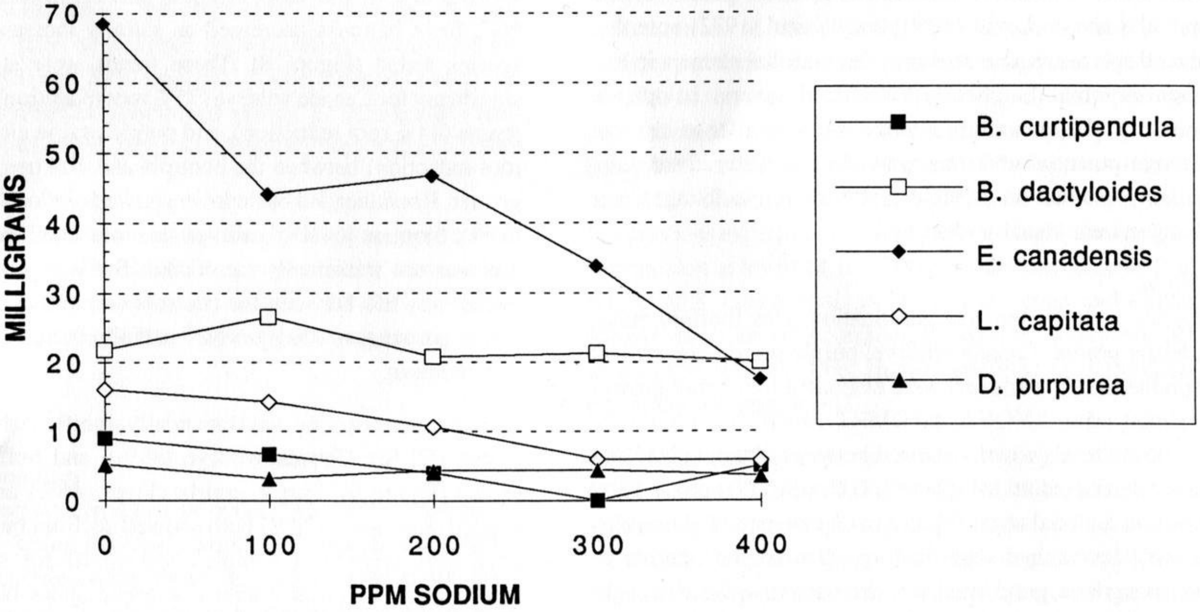


Figure 8. Root biomass response of five prairie species at Na$^+$ concentrations of 0, 100, 200, 300, and 400 ppm.

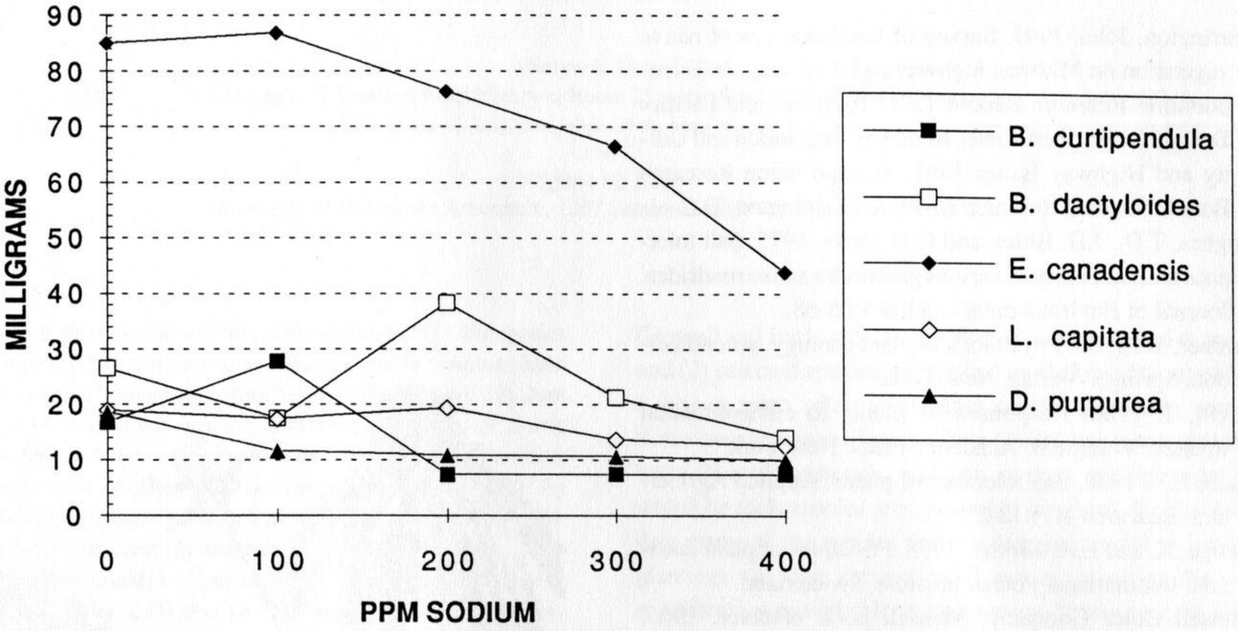


Figure 9. Shoot biomass response of five prairie species at Na^+ concentrations of 0, 100, 200, 300, and 400 ppm.

duced. Canada wildrye and buffalo grass appear to have the greatest tolerance to Na^+ of the species tested. Canada wildrye, in particular, demonstrated no loss of seedlings at 400 ppm Na^+. Both species had no decline in height at 400 ppm. Buffalo grass had no loss in root biomass and little in shoot biomass. Buffalo grass also had the least decline in germination of any species tested. On the other hand, Indian grass demonstrated the least tolerance of Na^+ when the measures of germination and seedling survival are considered.

The results of this study suggest the need for much more research. During the course of the study, the exact causes (osmotic potential, soil degradation, or direct toxic effect) of the responses were not determined. Soil dispersion and toxic effects, as might be indicated by foliage color, were not apparent. Changes in osmotic potential that affect water and nutrient uptake, although not investigated, are likely candidates for germination delays and, in the case of buffalo grass and sideoats grama, improved growth and survival (Unger 1982). Root depth was not studied, however, Na^+ declines with soil depth. For species that can quickly establish feeder roots below highly concentrated salt zones, road salt may not be a significant problem. This may be a factor why some seedlings of species in the study had high survival.

A second and essential need for further study is the confirmation of these results under field conditions. Larger soil volumes, weather patterns, differences in soil texture, presence of organic matter, and interspecies relations may all effect a species response to salinity. We have not initiated field experiments on germination. We are, however, conducting field experiments for Na^+ effects on established three year old plants of these species. Many more native species commonly used along roadsides also must be tested. Although this study evaluated eight species, the Wisconsin Department of Transportation currently uses forty-two species within plantings and plantings up to 70+ species are feasible and desired (Wisconsin Department of Transportation 1990). Finally, individual species must be examined for salt tolerance within their respective gene pools. Perhaps in areas where prairie species commonly grow along roadsides, selection for salt tolerance has occurred.

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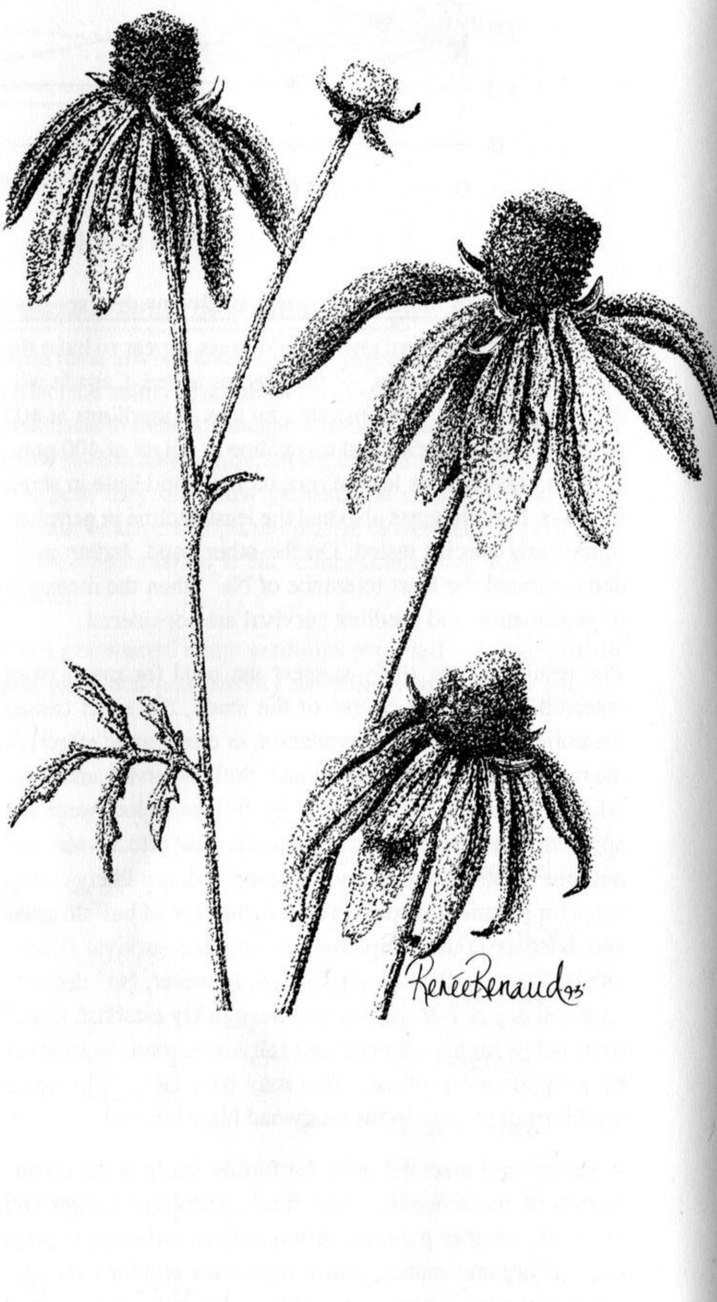

THE ROLE OF COMPETITION IN THE SUCCESSFUL ESTABLISHMENT OF SELECTED PRAIRIE SPECIES

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Abstract. In this study we addressed two questions: (1) Will species identified as being difficult to establish in prairie plantings have greater success if temporarily protected from competition? (2) Does the type of competition make a difference? We selected prairie species that are often unsuccessful in mixed-seed prairie plantings, and grew each of them without competition and with (1) big bluestem (*Andropogon gerardii* Vitman), (2) a mixture of easy-to-grow prairie forbs and (3) naturally invading weeds. Seeds of the competitors were added: (1) at the time of planting, (2) after a year with no competition, (3) after two or three years with no competition. Germination in the test plots was unexpectedly low, perhaps due to high mortality of moist stratified seeds during a dry spell that occurred after planting. Shooting star (*Dodecatheon meadia* L.) and prairie phlox (*Phlox pilosa* L.) had few or no germinants and were eliminated from the study. The germination of two of the remaining seven species, purple prairie clover (*Dalea purpurea* Vent.) and prairie dropseed (*Sporobolus heterolepis* A. Gray), was significantly affected by any type of competition the first year, and by weed competition whether the first year or later. Purple prairie clover was negatively affected, while dropseed was positively affected. The establishment of purple prairie clover and also of little bluestem (*Schizachyrium scoparium* (Michx.) Nash) was affected by the same two treatments: both were negatively affected. First year competition also significantly reduced in some species some of the attributes used as measures of vigor.

INTRODUCTION

Prairie restorations seeded on fairly good soils have a tendency to look alike during the first few years, often putting on a colorful display of such easily grown species as yellow coneflower (*Ratibida pinnata* (Vent.) Barnhart), black-eyed susan (*Rudbeckia hirta* L.) and bergamot (*Monarda fistulosa* L.). Other species included in the seed mix take longer to establish and flower, and there are always a few that never show up at all, even though they may frequently be seen in nearby prairie remnants. There has been little documentation as to whether the late-appearing species germinate initially and grow slowly, or whether they experience delayed germination (Howell and Jordan 1991). Similarly, little is known about why some species fail completely.

For some species the order in which species are added may be critical. Two general approaches have been distinguished (Howell and Jordan 1991): (1) all species are planted at once; and (2) selected species are planted and allowed to grow for a year or more, after which other species are added, sometimes over a period of years. Betz (1986) has advocated the latter "wave" approach, and has worked out the order in which he feels species groups should be added. He suggests that many of the species that are less successful in prairie plantings are "late successional" species requiring the site modification provided by easy-to-grow, "early successional (pioneer)" species. Such a relationship would fit the "relay floristics" succession model of Egler (1954).

It is also possible that a species may be unsuccessful not because it requires modified site conditions but because it cannot compete with weeds and easy-to-start prairie species. In this study we consider the possibility that the species that fail to show up in early years of seeded prairie restorations may be poor competitors --opportunists that must take advantage of chance events that at least temporarily provide a favorable situation without severe competition. To test this possibility, we used a "wave" approach, but in this case the first wave consisted of species identified as being difficult to establish in mixed prairie plantings. The second wave, consisting of one of three different types of competition, was added after predetermined intervals.

Thus, in this study we address two questions: (1) Will species identified as being difficult to establish in prairie plantings have greater success if temporarily protected from competition? and (2) Does the type of competition make a difference?

METHODS

Study Species and Competitors

We consulted publications, other prairie restorationists and our own experience to develop a list of 9 study species that frequently fail to appear when their seeds are planted as part of a prairie seed mix. (Table 1.) We used three types of competitors:

(1) a set of native prairie forbs that are quick to establish (wild indigo, *Baptisia lactea* (Raf.) Thieret; rattlesnake master, *Eryngium yuccifolium* Michx. (planted only in

1986); round-headed bush clover, *Lespedeza capitata* Michx.; yellow coneflower; black-eyed susan; prairie dock, *Silphium terebinthinaceum* Jacq.; and stiff goldenrod, *Solidago rigida* L. (planted only in 1986);

2) a native grass, big bluestem (*Andropogon gerardii* Vitman), known to do well in restorations;

(3) weeds--herbaceous plants that appeared spontaneously in the plots, dominant species being: love grass (*Eragrostis spectabilis* (Pursh) Steud.), chamomile, (*Anthemis cotula* L.), shepherd's purse, (*Capsella bursa-pastoris* (L.) Medic.), and purslane (*Portulaca oleracea* L.).

Study Site

The experiment was carried out in an area scheduled to become an addition to Curtis Prairie in the University of Wisconsin-Madison Arboretum. The site slopes very gently to the south and has well-drained silt loam soil--a good site for mesic prairie. It had served as a woody plant nursery for approximately 50 years. Prior to the initiation of the experiment, the ground was tilled 4 times in late summer and fall 1985 and 3 times in spring 1986 to reduce weed growth.

Experimental Design

We used a randomized complete block design with 4 replicate blocks of the following 10 treatments:

1. study species kept free of competition by hand-weeding for the duration of the experiment (1986 - 1989);
2. forb competitors introduced with the planting of the study species (1986);
3. forb competitors introduced 1 year after (1987) the planting of the study species;
4. forb competitors introduced 3 years after (1989) the planting of the study species;
5. grass competitors introduced with the planting of the study species (1986);
6. grass competitors introduced 1 year after (1987) the planting of the study species;
7. grass competitors introduced 3 years after (1989) the planting of the study species;
8. invading species (weeds) allowed to grow with the planting of the study species (1986);
9. weeds allowed to grow beginning 1 year after the planting of the study species (1987 on);
10. weeds allowed to grow beginning 2 years after the planting of the study species (1988 on).

Originally, the forb and grass competitors in treatments 4 and 7 were to have been introduced 2 years after the planting of the study species, but a severe drought in 1988 caused us to postpone the planting until 1989.

Each block contained 90 (1m x 1m) plots, making a total of 360 plots (9 species x 10 treatments x 4 replicates).

Seeding Pre-Treatments

Seeds of the 9 study species and the grass and forb competitors were gathered on restored Arboretum prairies in 1985 or purchased from local prairie nurseries. Seeds gathered in the Arboretum were stored through the winter in an unheated building. Prior to planting, the seeds were pre-treated according to techniques established in the literature as being best for each species. Pre - treatments included scarification and dry or moist stratification for periods of 5 to 12 weeks (Table 1). Seeds of each legume species were inoculated with appropriate nitrogen-fixing bacteria.

All seeds were tested for viability on moist paper in petri dishes, and in flats. All of the species germinated in these tests, and in general, the germination rates of the study species were similar to those of the planted competitors. Figures for per cent viability and seed weight for each species were used to calculate the weight of seed needed to produce approximately 10 plants of the study species for each experimental plot. For three of the species -- needle grass (*Stipa spartea* Trin.), prairie phlox (*Phlox pilosa* L.), and compass plant (*Silphium laciniatum* L.) -- we were unable to obtain the desired number of seeds and planted smaller amounts.

Planting Procedures

Study species and competitors were assigned to plots using a stratified random procedure.

The study species were hand-planted by Arboretum volunteers May 29 - 30, 1986. Because 3 of the study species --including shooting star (*Dodecatheon meadia* L.), as well as the sparsely planted needle grass and phlox --showed little or no germination in the plots, these species were replanted on July 9, 1986 with freshly harvested seed. As these were spring - flowering species, we speculated that the seed harvested in 1985 may have lost viability during the long storage period. Forb and grass competitors were hand-seeded into appropriate plots on May 29 - 30, 1986 and 1987, and June 5, 1989. Plots were weeded by hand so that each contained only the species planned for that plot -- a single study species and the appropriate competitors.

Data Collection and Analysis

New germinants were recorded in all of the plots in June, July or August, and October from 1986 to 1989. Individuals were marked as they appeared so that the year of origin was clear.

Table 1. Planting and germination data for study species.

	Weight of seed planted g/plot	Number of seeds planted per plot	% of seed moist stratified	Period of moist stratification (wks)	Number of germinants per plot	Total Number of germinants	% germination
FORBS							
Amorpha canescens Lead Plant	1.25	484	100	11.5	1.0	39	0.2
Baptisia bracteata Cream Wild Indigo	4.90	343	69^1	7.5	5.3	210	1.5
Dalea purpurea Purple Prairie Clover	2.50	1585	100	11.5	5.2	207	0.3
Dodecatheon meadia Shooting Star	0.25	670	24	4.5	0	0	0
Phlox pilosa Prairie Phlox	0.09	25	100	11.5	0.2	7^2	0
Silphium laciniatum Compass Plant	3.65	102	52	4.5	2.1	82	2.0
GRASSES							
Schizachyrium scoparium Little Bluestem	2.00	1130	0	-	-	-	-
Sporobolus heterolepis Prairie Drop Seed	1.00	560	0	-	1.5	60	0.3
Stipa spartea Needle Grass	1.78	500	70	4.5	5.0	198^2	-

^{1} Seed also scarified
^{2} Some or all from second planting

Each year at the time of flowering (generally June and September) counts of individuals or, in the case of little bluestem (*Schizachyrium scoparium* (Michx.) Nash) for which "individuals" could not be readily identified, visual aerial cover estimates, were made. Measurements to give an estimate of the vigor and reproductive effort of the study species were also recorded. The measurements varied with the morphology of the species, and included height, number of stems, cover, number of flowering individuals, number of flowering stems, and number of flowers per flowering stem. Data were analyzed by analysis of variance (SAS 1985). Results were considered significant at the p = 0.05 level.

RESULTS

Germination of the Study Species

Germination of forbs was extremely low (Table 1). The highest value was 2% for compass plant; two species had virtually no germination. Among the grasses, prairie dropseed (*Sporobolus heterolepis* A. Gray) had a low rate, within the range for forbs. Needle grass plots were replanted with freshly gathered seed because no germinants had been found by midsummer of the first year. At the end of the four year experiment, 198 germinants had appeared, but it was not possible to determine how many resulted from the second planting. Little bluestem was the most successful species in germinating. Seedlings appeared in each of the forty plots in which they were planted; there were so many that it was impractical to count them and we recorded cover instead.

Compass plant had new germinants each of the four years (Table 2). Cream wild indigo (*Baptisia bracteata* Elliott), purple prairie clover (*Dalea purpurea* Vent.) and needle grass germinated in three of the four years, including the fourth year, and the latter two species had substantially more germination the second year than the first. Lead plant (*Amorpha canescens* Pursh.), however, germinated primarily in the first year.

Both the time when competition was added and the type of competition affected germination of purple prairie clover. The mean number of germinants/plot for this species was 3.4 when competition was added the first year, compared with 8.2 when competition was delayed until the second year and 9.7 when competition was delayed until the third and fourth years. These differences were statistically significant ($p < 0.05$). When grown with weeds as the competitors, purple prairie clover had 4.3 germinants per plot. This was statisti-

Table 2. Survival of germinants.

	Number of 1986 germinants present in fall of:				Number of 1987 germinants present in fall of:			Number of 1988 germinants present in the fall of:		Number of 1989 germinants present in the fall of:
	1986	1987	1988	1989	1987	1988	1989	1988	1989	1989
Amorpha canescens Lead Plant	36	14	16	16	3	3	3	0	0	0
Baptisia bracteata Cream Wild Indigo	167	56	44	50	37	22	21	0	0	6
Dalea purpurea Purple prairie clover	49	35	37	38	149	97	92	0	0	9
Silphium laciniatum Compass Plant	41	32	33	34	16	19	20	10	9	15
Sporobolus heterolepis Prairie Dropseed	56	25	22	21	4	4	4	0	0	0
Stipa spartea Needle Grass	66	44	41	41	80	79	70	36	34	16

Numbers reflect totals from all plots

cally different from the 9.7 germinants per plot produced when the competitor was big bluestem grass. Forb competition produced 7.3 germinants per plot, an intermediate number not significantly different from either of the other two.

Statistical analysis indicated that prairie dropseed germination was significantly increased by first year competition and by weed competition. (The problem of identification of dropseed seedlings the first year is a factor that should be considered in evaluating these results.) First year competition plots had 9.6 germinants per plot, significantly different from the 2.8 per plot when competition was delayed until the second year and the 5.8 per plot when it was delayed until the third and fourth years. Plots with weed competition had 9.2 germinants per plot, while with forb and grass competition the per plot values were 5.1 and 3.8.

Establishment of the Study Species

Table 2 shows the number of individuals remaining each year in each cohort by species (all treatments combined). Compass plant showed the best survival; of a total of 82 germinants, 78 (95%) were present in 1989 at the end of the experiment. In general, if a species sustained substantial losses, it was between the first and second years, and, with the exception of purple prairie clover, 1987 germinants survived better than 1986 germinants.

Note that in some years some species appear to have more survivors than were present the year before. Although recording errors may be involved, our observations suggest that some plants did indeed become dormant under unfavorable conditions (the drought in 1988 for example) and then produced new shoots the next year.

Table 3 shows the number of individuals present (in the case of little bluestem, % cover) in 1989 by treatment. An inspection of Table 3 reveals trends toward poorer establishment of little bluestem and purple prairie clover when any type of competition was added the first year or when the type of competition was weeds. These differences were statistically significant ($p < 0.05$).

Other Effects of Treatments

First year competition also significantly reduced the number of stems, the number of flowering stems and the height of purple prairie clover; the cover, number of stems and height of compass plant and cream wild indigo; and the cover and number of flowering stems of needle grass.

There were significantly fewer stems and flowering stems of purple prairie clover when grown with weeds than when grown with forbs or big bluestem, while the height of compass plant was reduced by forb competition.

No other differences were statistically significant.

DISCUSSION AND CONCLUSIONS

The study was hindered by low germination rates (and in two cases, lack of sufficient seed to achieve the desired planting density), which made statistical tests problematic. The discrepancy between germination rates in the tests and in the field was unexpected and is difficult to explain. It is possible that the additional time in storage reduced the viability of the

Table 3. Number of individuals of each study species in each treatment present in fall, 1989. Data for *Schizachyrium scoparium* are % cover.

Type of competition	Weed			Forb			Grass			None
Year competition started	1986	1987	1988	1986	1987	1988	1986	1987	1988	
No. of growing seasons without competition	0	1	2	0	1	3	0	1	3	4
Number of individuals of										
Amorpha canescens Lead Plant	0	7	4	1	1	0	2	1	2	1
Baptisia bracteata Cream Wild Indigo	2	6	11	1	15	8	11	8	4	11
Dalea purpurea Purple Prairie Clover	0	3	11	3	26	16	7	26	31	16
Silphium laciniatum Compass Plant	11	9	9	1	5	8	6	9	9	11
Sporobolus heterolepis Prairie Dropseed	0	1	7	0	0	7	2	2	0	6
Stipa spartea Needlegrass	19	27	17	33	11	11	2	14	9	18
Mean % cover of:										
Schizachyrium scoparium Little Bluestem	15.0	43.8	62.5	36.3	93.8	97.5	28.8	97.5	97.5	97.5

seeds. In addition the seeds for the germination tests were more carefully screened visually to be sure the seeds were well developed. Some allowance for this was made in the calculations to determine the amount of seed per plot, but perhaps that was insufficient.

The dry period which occurred after planting is another factor to consider. This may have caused high mortality of moist stratified seeds. In support of this possibility is the correspondence of high percentage of seeds moist stratified with especially low germination rates for the forbs that germinated. (Table 1)

The data show that, at least under the environmental conditions of this study, competition during the first year and weed competition any year were the most important of the factors studied in reducing germination and establishment success. Purple prairie clover and little bluestem were the species most affected by these factors. This is a useful addition to the rather limited information available on the culture of individual prairie species. The study may have practical application for managers; for example, it appears now that the reason for two puzzling repeated prairie planting failures on an arboretum site is the use of a seed mix in which little bluestem was the dominant grass, without provision for weed control adequate for little bluestem, a species that appears to be particularly vulnerable to weed competition.

The importance of weed competition on the experimental site is somewhat surprising, in view of the elaborate site preparation, and the apparent excellent success of a prairie planting carried out on the part of the site not occupied by the experiment. The weeds that did appear in spite of the multiple cultivations prior to planting were mostly species not known to persist in prairie plantings. Even so, they affected little bluestem and purple prairie clover, and perhaps other species.

In the Henry Greene Prairie, in many ways the most successful of the Arboretum prairies (Kline 1992), there is an area where eight of the study species (all but needle grass) are growing together. The area is notably lacking not only in weeds but also in big bluestem, as well as the easy-to-establish forbs of this study and any other of the more aggressive prairie species. All eight of the species are flourishing; each obviously tolerates the competition of the others. The site is somewhat wetter than that selected for this experiment, which may be an important factor in discouraging other competitors. It may be important, nevertheless, to follow this study with an experiment in which a fourth group of "competitors" is tested--a group of similarly difficult-to-establish-species. Such a group of species would not be likely to be too competitive with each other, but might provide some site amelioration and possibly some weed discouragement.

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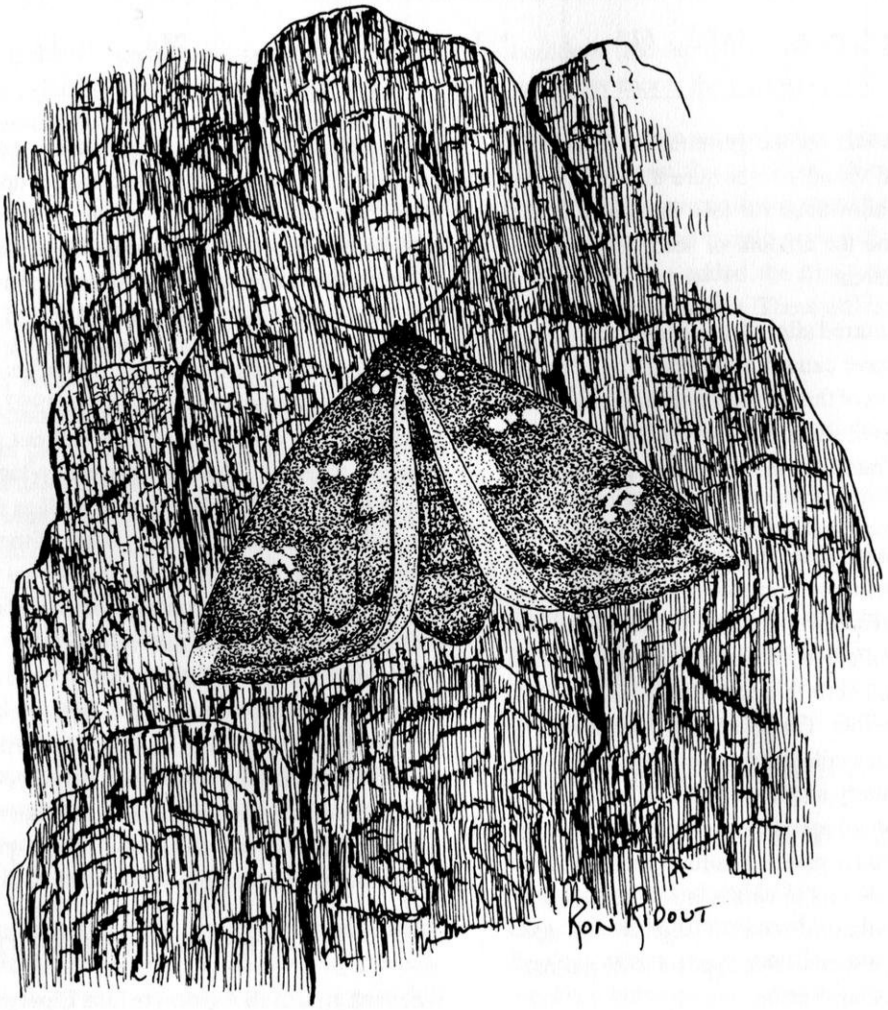

A SIMPLE THREE-DIMENSIONAL CLASSIFICATION SYSTEM FOR PRAIRIE MANAGEMENT

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Abstract. A prairie classification system was developed for use by any grassland manager. This system projects a grassland onto three-dimensional coordinates. The vertical continuum is from tame to successional. One horizontal continuum is from xeric to hydric species. The projecting continuum is from exotic to native. These coordinates give a general yet quantitative impression of a whole prairie on the basis of its ranges over three dimensions. This system describes past and present and suggests future management.

INTRODUCTION

We often think that a gap exists in our ability to describe prairies. The words 'native prairie,' 'natural prairie,' 'original prairie,' 'native prairie grass,' 'prairie restoration,' 'prairie re-construction,' have been applied to so many kinds of plantings and landscapes that the words have lost much of their meaning. The only alternative appears to be a quantitative vegetational analysis. There are three problems with quantitative types of prairie description. First, few prairie managers have the time, money and skill to conduct such an analysis. Second, the abstract nature and complexity of the results makes it difficult to communicate this information to all those involved in the management of our prairies, especially the general public and funding agencies. Lastly, few if any of these descriptions include a perspective of the management history of the prairie.

Having heard many individuals voice this same concern, we decided to propose a method of describing prairies to fill this gap.

Can each unique mix of plants and animals be described? Could a clear, accurate description help define management goals and strategies for each area - and even for smaller areas within a defined prairie? Might it help ecologists define the characteristics of a grassland in a way that can be easily, and accurately conveyed to other scientists? We suspect that such a system is not only possible, but potentially viable.

METHODS

Figure 1 is our suggestion for such a system. Mathematicians would call it a "three-dimensional Cartesian coordinate system." The vertical ("Y") axis represents the management history of a prairie area. The horizontal ("X") axis represents the moisture levels, from extremely wet to extremely dry. The projecting, three-dimensional ("Z") axis represents the origin of the species composition, ranging from exotic to native species.

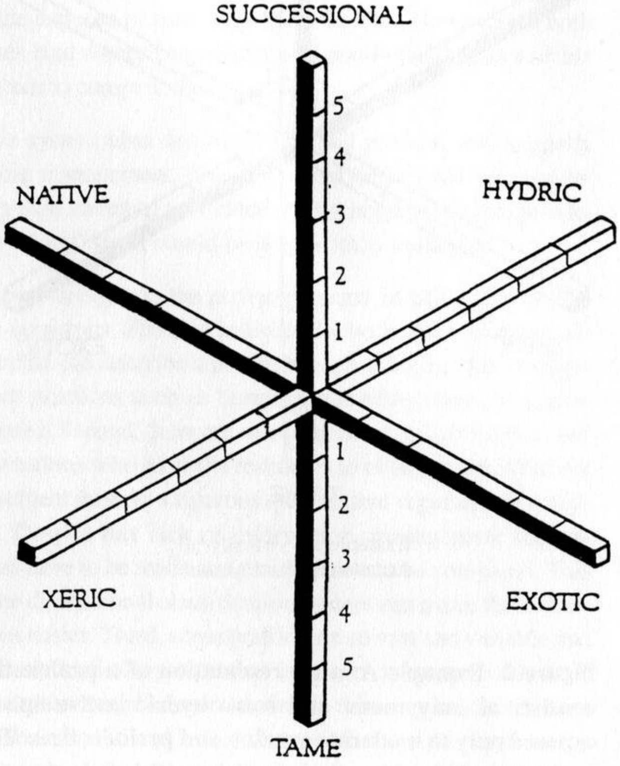
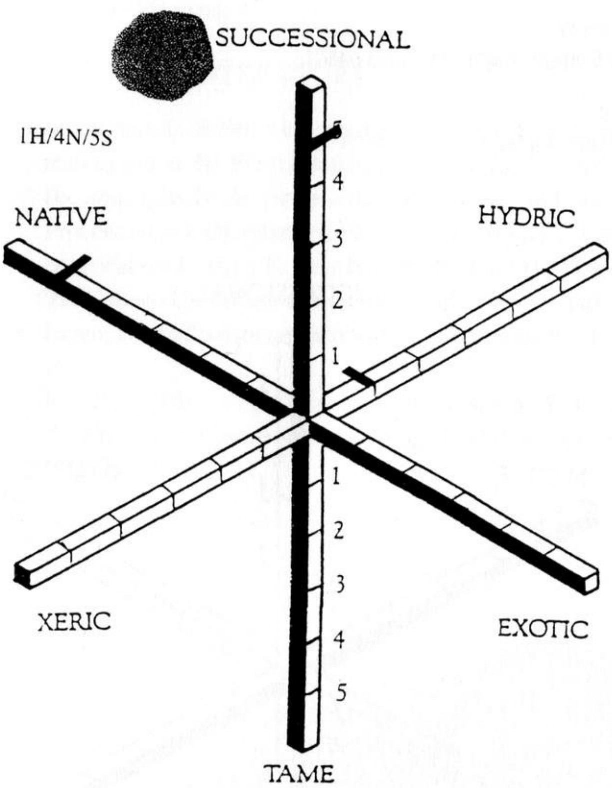


Figure 1. Three-dimensional prairie classification system. The vertical axis represents the management history of a prairie area. The horizontal axis represents the moisture range. The projecting, three-dimensional axis represents the species composition, ranging from exotic to native species.

The justification for the vertical axis comes from Smith (1990) who suggests two categories of grassland: tame and successional. These two can be said to describe the "conservation" history of a prairie. A successional grassland, as the name suggests, shows a naturally-generated progression to-



Example A: virtually all successional and native

Figure 2. Example A: a representation of a prairie that consists of only mesic and some hydric native species exposed only to moderate grazing and periodic fires. This prairie would be given the coordinates "1 hydric, 4 native, and 5 successional" (1H/4N/5S).

ward a self-maintaining, stable climax community. The obvious example is a pre-settlement tallgrass prairie, usually with periods of increased or decreased tree invasion. On the other hand, a tame grassland owes its existence to agricultural management practices (such as mowing and planting with a seed drill). These two theoretical extremes, with "TAME" at one end and "SUCCESSIONAL" at the other, represent one axis of the 3-D system.

The next continuum describes the moisture regime of a site. There are (according to Smith (1990) and Schroeder (1981)) two further characteristics: at one extreme, a xeric prairie gradually turns into dry uplands, glades, and finally barrens. This area has dry, usually stony soil that only accommodates the most drought-resistant prairie plants and animals. A very different balance of plants are found on a hydric prairie, which gradually grades into riparian meadows too wet for most prairie plants. This prairie continuum, from xeric to hydric, represents the second axis of the prairie 3-D system. This line on the graph would have "XERIC" at one end and "HYDRIC" at the other.

Finally, each prairie area has its own mix of species, as represented by the projecting or 3-D axis. This describes the species composition on the basis of origin. An area's composition can range from the receding "NATIVE" end (exclusively native species) to the projecting "EXOTIC" end (exotic introduced species).

This system can be applied in relatively subjective or objective ways. An example of a subjective application of this classification system would involve six steps. First, several random locations would be identified in the prairie to be classified. The number of locations would depend on the size and variability of the prairie. Second, the management history of each location would be determined by the use of land use records, aerial photographs, and interviews with local individuals (Jackson 1990). This management history would be represented by a relative point on the range from tame to successional. Third, the moisture regime of each location would be determined from a subjective evaluation of the topography, slope, aspect, soil texture, soil type and relative moistness of the soil. A county soil survey would be helpful in this evaluation. This moisture regime would be represented by a relative point on the range from hydric to xeric. Fourth, at each location 40 identifiable plants chosen at random would be characterized as native or exotic. The ratio of exotic plants to native would be represented by a relative point on the range from native to exotic plant composition. Sixth, each location would be represented by a single point on the 3-D continuum. The points from each location would be presented on a single 3-D graph, and the prairie would be represented by a "cloud" of points that defines the community.

DISCUSSION

In order for as many people as possible to use this system, we have tried to make this a fairly simple, descriptive, three-dimensional way to describe a prairie. The botanical makeup of any particular square meter could be pinpointed at a certain spot, while the 2,000-acre prairie surrounding it would need a "cloud" of characteristics.

Every area of grassland would have its own "personality" in this 3-D system, and there would be many ways to classify the grassland on the basis of the coordinates. One way to gather data for this type of classification could be a thorough visual survey of a grassland coupled with interviews of area landowners. This, for example, might reveal a prairie that consists only of native mesic and some hydric species exposed only to moderate grazing and periodic fires for as long as anyone can remember. You would be justified in describ-

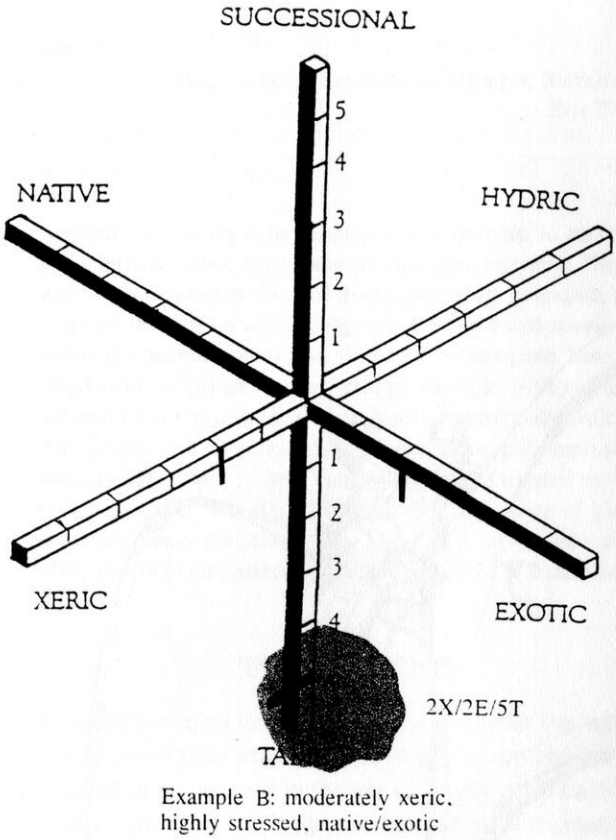


Figure 3. Example B: a representation of a moderately xeric- adapted species mixture consisting of 70% exotic species and 30% native species with a long history of agricultural management. This grassland would be given the coordinates "2 xeric, 2 exotic, and 5 tame" (2X/2E/5T).

ing this area as 1 hydric, 4 native, and 5 successional (1H/4N/5S) as long as you described how you analyzed the area (Figure 2, example A:).

Our recently finished quantitative vegetational analysis of a grassland in England provided a second way to gather data for this type of classification. We applied the 3-D classification system to management units identified by a clustering algorithm using importance values derived from sample plot analysis. This was not a comparison of these techniques but rather the algorithm results provided the data to construct the 3-D classification of the area. The cluster analysis indicated four distinct units. Using one of the units as an example, these techniques indicated a moderately xeric adapted species mixture consisting of 70% exotic species and 30% native species. The area has had a long history of agricultural management practices. Figure 3 (example B:) shows that we characterized this area as 2 xeric, 2 exotic, and 5 tame (2X/2E/5T). The advantage of describing the algorithm results with the graph in Figure 3 is that the graph shows at a glance the results of the analysis.

The reliability of this classification system is equal to the reliability of the sampling techniques used to obtain the data that determines the coordinates. In the first example, sampling bias, quantitative accuracy, and boundary questions make the conclusions less reliable. However, the analysis was fast and communicated the conclusions very well. In the second example, the reliability is as good as can be expected at the expense of time, money, and effort. However, in both cases land owners, managers, and non-botanists can use this system to compare the two areas.

This system also describes past and present, and suggests future management. If an area described on the 3-D system was then enlarged to include a very large or diverse prairie, the "cloud" itself would be dramatically enlarged.

The advantages to the prairie manager in using this system are numerous. First, an individual who is not a professional botanist can describe a prairie to such a degree that management practices such as burning or seeding could be implemented. Second, there are many agencies, organizations, and institutions who have the resources to obtain prairies but not to subject them to a rigorous quantitative vegetational analysis. Despite this lack of information, management suggestions have to be made and prairies have to be compared. This three dimensional classification system can make these decisions easier. Third, some prairies are so vast and variable that a classification system that is broad in scope with little resolution might be more desirable than a quantitative vegetational analysis of selected areas. Lastly, this system can present at a glance what otherwise would involve the interpretation and synthesis of several numbers.

An additional advantage of the 3-D classification technique is that it is portable. We feel that it can be used equally well in describing the grassland of England as well as the short, mixed and tallgrass prairies of the United States.

It is presumptuous to suggest reducing the tremendous variety of any grassland to a simple graph. However, we hope that this system can encourage people to consider the prairie continuum in a new and brighter light, give scientists a more accurate way to compare field notes, and help managers use a management strategy that is most effective for a given purpose. We welcome any criticism or suggestions concerning this mechanism of grassland classification.

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COOPERATIVE RARE PLANT RECOVERY IN WISCONSIN

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Abstract. Wisconsin is developing a new program to encourage public/private sector cooperation in rare plant recovery. The program allows interested persons to experimentally propagate, raise, outplant and sell certain endangered and threatened species. By utilizing a permit system, the Bureau of Endangered Resources (BER) will coordinate recovery efforts statewide. BER will assure the use of local seed stock, prevent genetic contamination of extant populations, and keep records of plant sources and outplantings. Documentation will prevent confusion between planted and wild populations and will allow for long-term monitoring of planted sites. Gardeners purchasing rare plants will receive educational materials about rare plants and will be integrated into the recovery program.

INTRODUCTION

Increasing interest in the use of native plants for landscaping and for restoration and recreation of natural communities has resulted in an increase in the use of locally or globally rare plants. Gardeners and landscapers interested in the plants are sometimes unaware that these species are rare. Other native landscapers and nursery owners use or grow these plants to diversify the landscape. Rare species are also used by restoration ecologists who are trying to restore a full assemblage of species that may have once occurred in the community. There are also botanical researchers who are specifically interested in rare species work and are searching for methods for establishing new populations of rare plants. This wide array of interests provides a great opportunity to work with a range of individuals, from professional botanists to gardeners. We will be able to learn from their experiences and to share with them information on various aspects of plant conservation and recovery.

Goals and Objectives of the Rare Plant Recovery Program

The goal of the Rare Plant Recovery Program is to maintain within Wisconsin uncultivated, viable populations of endangered and threatened plant species and their inherent genetic diversity through protection of the habitats and natural processes that sustain them.

Objectives regarding outplanting and recovery:

1) Protect the habitats and natural processes that sustain rare plant populations.
2) Identify naturally occurring populations of endangered and threatened plant species and protect native populations from destruction and exploitation.
3) Maintain viable population sizes throughout the range of the species in the state.
4) Protect the genetic integrity of naturally occurring populations against outbreeding depression by plants introduced from other populations, and against inbreeding depression from populations becoming too small and isolated.
5) Document the location of and monitor the success of outplantings to non-garden plantings to ensure that resources (e.g., acquisition, management, environmental review, mitigation, etc.) are directed in the future toward protection of naturally occurring, rather than planted populations.
6) Encourage a coordinated approach by private citizens, organizations, businesses and public agencies towards preservation and management of our endangered and threatened flora.

Development of the Rare Plant Recovery Program

There are concerns regarding widespread collection and use of rare plants in the landscape that need to be addressed. These include: potential genetic contamination of existing populations by the introduction of non-local ecotypes, documentation of propagule sources and outplanting locations, and legal limitations. The Wisconsin Department of Natural Resources (WDNR) assembled a Plant Policy Advisory Committee to assess the current situation and define a program that could be developed to enhance cooperative rare plant recovery work. This committee is composed of individuals from several programs within WDNR, university ecologists, plant taxonomists, and representatives of the native plant nursery and restoration industry.

Currently, in Wisconsin it is illegal for anyone to process or sell plants legally listed as endangered or threatened by the state of Wisconsin without a permit from the WDNR (Wis. Statutes 29.415). The statute restricts permits to uses of plants for preservation, scientific and educational purposes. Minor aspects of the accompanying rules prevent commercialization by requiring that persons purchasing rare species possess an endangered and threatened species permit (Wis. Administrative Rules, Chap. 29).

In order to assess interest in the use of rare species, the committee surveyed native plant nursery catalogs and species lists for ecological restoration projects. Committee members also met with nursery growers and restorationists about their interests and needs. This resulted in a list of rare species which were being grown by nurseries and species for which there is interest in the near future. The committee found a range in the source of propagules being used. Many native plant nurseries and restorationists utilize only local ecotypes for restoration projects. Other nurseries, primarily the larger more traditional companies, sold species which are rare in Wisconsin, but very common in the commercial nursery trade. The original geographic source for many of these commonly grown plants is often uncertain.

In the past, endangered and threatened species permits have been granted primarily for research and inventory purposes and have not been issued for commercialization of rare species. Nurseries and restorationists are interested in legally growing, selling and utilizing rare species. Interested parties desire to assist in the establishment of new rare plant populations. Some individuals are interested in augmenting existing populations by introducing new genetic material.

Some researchers and restorationists document the exact source and ultimate destination of rare plants being propagated and planted into native communities or restorations (BER 1992, Apfelbaum personal communications). However, commercial sales of rare species have resulted in little documentation in relation to source or planting location. Documentation of propagule source and planting sites is critical to distinguish native populations from planted populations for research and protection purposes. It is important to conduct long-term monitoring of planted populations to evaluate if plants will become established and are self regenerating. Provided sufficient established plantings are documented to be viable it is possible that a species could be removed from the endangered and threatened species list.

The nursery industry has indicated to the committee that it is important to keep paperwork in this program to a minimum. This was one of the goals for developing an expanded permitting program to provide for the commercialization of rare species.

The primary concern of the committee is the distribution and out-planting of rare plants with regard to the biotic and abiotic needs of the individual species. In order to assess these needs it is necessary to determine the causes of plant rarity which may be caused by one or more of the following factors:

- Loss of habitat
- Degradation or fragmentation of habitat
- Over-collection of rare plants
- Wisconsin is at the edge of a species natural range
- Unique micro-habitat requirements
- Relic populations from an earlier geological time

Species which are rare in response to habitat loss or degradation, and species on the edge of their range in Wisconsin are not as critical a concern for protection from possible genetic contamination. Permitting for commercialization is more likely with these species. Species requiring very specific micro-habitats or relic populations of a species with few other populations within the habitat type may be genetically unique and will not be permitted for sales or distribution. Lapland rosebay (*Rhododendron lapponicum* (L.) Torr) is an example of the latter category. Lapland rosebay is found in two very small populations in Wisconsin with the nearest neighboring population located in New York State (Read and Wrzeninski 1978).

There is also concern about the genetic mixing of distinct genotypes of different wild sub-populations on one species. Northern monkshood (*Aconitum noveborascense*) has been found to have unique genetic characteristics from different valleys within a few square kilometers (Kuchenreuther personal communications). Species like northern monkshood may have developed genetically diverse subpopulations as an adaptation to different microclimates.

Genetic swamping of extant populations by non-native or non-local ecotypes can be of concern for species on the edge of their range. Some of these populations have evolved adaptive characteristics to compete and survive within marginal habitats. With the introduction of genetic material from closer to the center of the range of the species, these unique adaptive characteristics may ultimately be lost and the population may decline or disappear.

The potential for over-collection of plants or seeds from the wild is of concern. Currently, there is limited coordination between individuals who collect seeds from various sites. A centrally located permitting system would allow for coordinated collection. This system would also provide the documentation necessary to distinguish wild from planted populations and to monitor demographics and survival of outplanted populations.

Implementation of the Rare Plant Recovery Program

An endangered and threatened species permitting program is being developed to allow for controlled and limited propagation and use of rare species. It will provide permits for applicants specifically interested in propagating or utilizing rare species for preservation, scientific or educational purposes. Individuals, organizations or businesses may submit an application to the WDNR. Only entities justifying their plans for the three purposes listed above will be granted a permit. This application will include names of the rare species to be used, intent of the project, and source of propagules. The committee and department staff will review the applications and develop individualized permits for applicants. These permits indicate what species may be grown and will include conditions that may be placed on the collection, growth, or distribution of these plants. Permit conditions vary based on the needs of the species and applicants involved. For select species, permits will be granted only for experimental propagation and/or planting as part of a cooperative recovery effort. Species commonly utilized in restorations may be allowed to be sold by permit holders. All entities receiving an endangered and threatened species permit are required to submit an annual report. The permit program will allow individuals without permits to purchase these plants from legally permitted nurseries.

Nurseries possessing permits will record the names and addresses of the persons who purchase listed plants, and will also provide the buyers with written information about these species, and their role in the rare species recovery program. If the purchaser uses the plants in a wild natural remnant or a restoration which could potentially be confused with wild populations in the future, they will be asked to voluntarily submit documentation for the location and source of such plantings. Long-term monitoring of the status of these populations will be possible.

CONCLUSION

A number of administrative rules must be revised prior to initiating this program. The permitting program is scheduled to be in place by the spring of 1993. The program will then work with persons around the state to recover rare species and to encourage their interest in plant conservation. Eventually we hope to work with many individuals and organizations to restore threatened or endangered floristic species critical to the healing of this planet.

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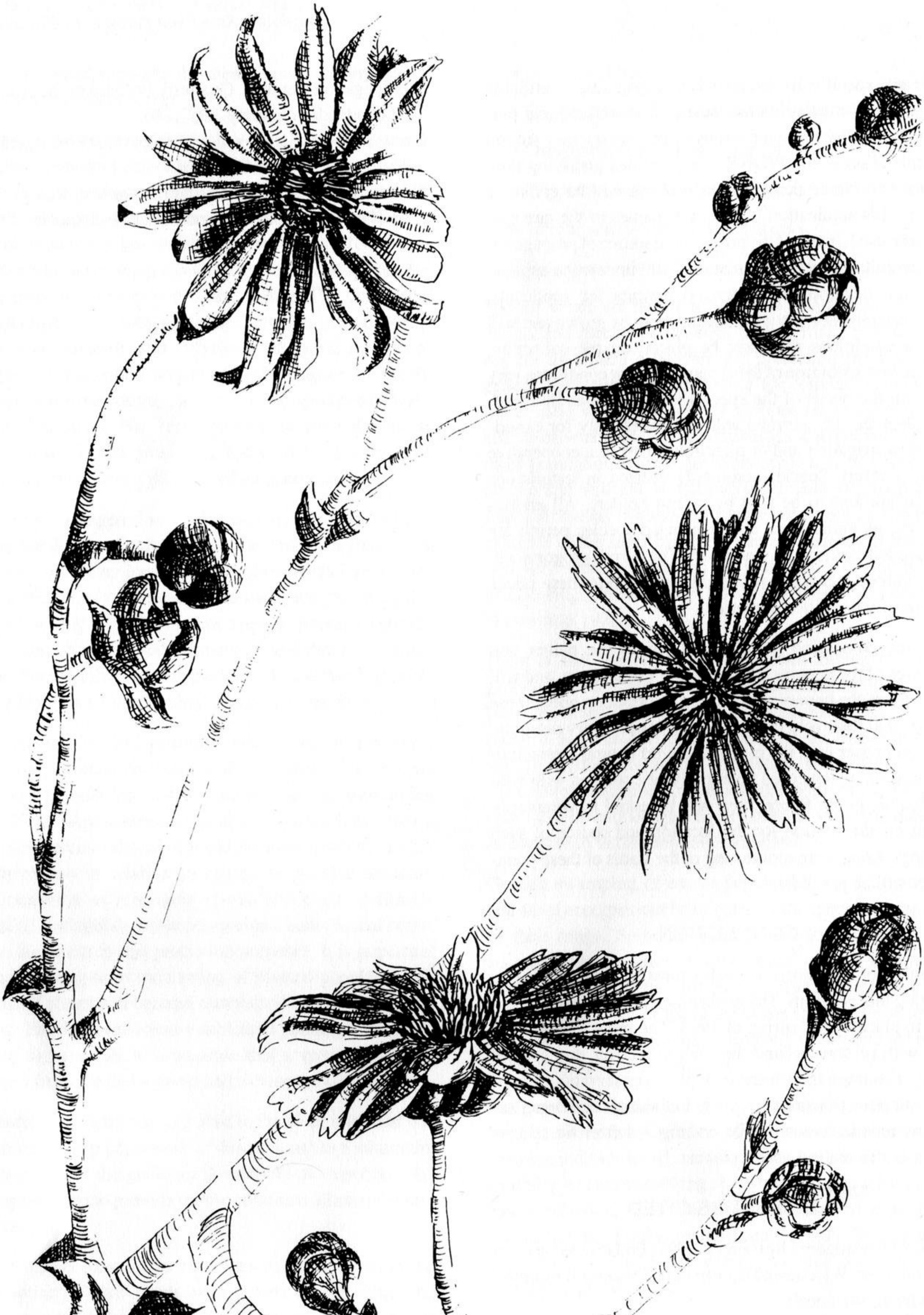
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EFFECT OF BURNING ON A DRY OAK FOREST INFESTED WITH WOODY EXOTICS

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Abstract. Fire was reintroduced into a 10-hectare dry oak forest dominated by a hybrid black oak (*Quercus velutina* X *Q. ellipsoidalis*) and heavily infested with honeysuckle (*Lonicera* X *bella*) and buckthorn (*Rhamnus cathartica*). The forest had been a fire-maintained savanna before settlement. Prescribed burns in 2 consecutive years followed by a year with no burn were accompanied by: a decrease in tree density and basal area per hectare during the two burn years that was balanced by increases during the no-burn year, resulting in little net change; a change in the size distribution of black oak (higher top-kill of small trees) and a substantial decrease in black oak tree density; a large reduction in number of saplings of black oak, white oak and black cherry; a decrease in cover of honeysuckle and buckthorn in each of the burn years, followed by a slight increase in the year of no burn; increased diversity of ground layer, including increases in woodland, prairie and exotic species - the woodland species being better represented and showing the greatest increase. We conclude that prescribed burns can suppress honeysuckle and buckthorn and encourage a more diverse ground layer dominated by native species. With frequent burning, tree density may decrease slowly through selective top-kill of younger trees and saplings. Black oak will continue to dominate in the foreseeable future, but with fewer, larger trees. Continued increase in ground layer diversity will depend on availability of propagules and, for the prairie species, of sufficient light.

INTRODUCTION

Before European settlement, oaks grew in a continuum of fire-adapted communities in southern Wisconsin and elsewhere in the "Prairie Peninsula" (Transeau 1935, Curtis 1959, Kline 1985, Anderson 1991). Tree densities varied from open prairie with less than 2.5 trees per hectare to oak forests with more than 250 per hectare. Intermediate segments along the continuum have been put into various categories, such as "savanna" and "oak woodland" (Curtis 1959, Packard 1991) but the boundaries were not discreet. Nor were they stationary, rather, they fluctuated over time in response to long and short term climate fluctuations and the frequency and intensity of fires. In the absence of fire, the trend is toward forest, and the oak forests of southern Wisconsin are examples; most were savannas when the settlers arrived but with the ensuing cessation of fire have become forested.

We have reintroduced fire into such an oak forest, with two main objectives. The first is to restore a process (fire) that was an important factor in shaping the community. The forest is to be part of a 60-hectare fire-managed mosaic of prairie, savanna and oak forest (Figure 1) with gradual transitions between the communities--a landscape similar to the presettlement condition. Stritch (1990) has begun similar restorations of the presettlement mosaic in southern Illinois and stresses the importance of landscape scale prescribed burns. The second objective is to determine the effectiveness of prescribed burning in controlling a severe infestation of honeysuckle (*Lonicera* X *bella*) and buckthorn (*Rhamnus cathartica*). Fire has been recommended as the preferred control method for buckthorn where the natural community will not be adversely affected (Heidorn 1991).

Grady Knolls Forest, the site selected, is a 10 hectare (24.7 acre) oak stand located on an end moraine, with sandy soils and 2-10% slopes, generally southerly. Before settlement the vegetation was oak barrens, a savanna of sandy soil. Most of the open grown oaks were a hybrid of black oak (*Quercus velutina*) and Hill's oak (*Q. ellipsoidalis*), with some white oak (*Q. alba*) and bur oak (*Q. macrocarpa*). The site was grazed until acquired by the Arboretum in 1940. At that time there was an open stand of widely spaced oaks on the site, most of them dating from the time the frequent wildfires stopped. Cessation of grazing allowed growth of abundant young oaks. In 1946, and again in 1954, wildfires ignited by passing trains burned across the intervening prairie and through the forest, top-killing the small oaks and many of the large ones. There was vigorous resprouting, especially of the younger oaks. Additional large trees were killed by oak wilt (*Ceratocystis fagacearum*), creating a large gap in the center of the woods. When the prescribed burns began in 1990, the remaining large trees were surrounded by younger oaks, along with vigorously invading black cherry (*Prunus serotina*). The shrub layer consisted of nearly continuous, almost impenetrable honeysuckle and buckthorn, and the ground layer was sparse. In this paper we describe changes that took place after prescribed burns were carried out in 1990 and 1991, both times in the spring.

Table 1. Changes in total saplings and trees (Figures are combined totals for all plots sampled).

	No. Saplings	No. Trees	BA(dm^2) /Tree	BA(dm^2) /ha
1989	375	160	3.5	1419
1990 (Burn)	297	147	3.7	1358
1991 (Burn)	306	135	4.0	1344
1992	260	160	3.6	1449

BA = Basal area

METHODS

Location of sample quadrats was facilitated by prior establishment of markers (aluminum-capped monuments and 1.5 m fence posts) at the corners of a grid of 0.25 ha squares (Figure 2) that eventually will be established throughout the arboretum. The "Arbgrid" will be useful for mapping vegetation and for accurately locating sites of research and management activity. It is a critical component of the arboretum's geographic information system (GIS), a computerized system allowing linking of maps and database information for enhanced spatial analysis.

A 200-m^2 plot was laid out in the southwest corner of each grid square, for a total of 20 plots. If a firelane was found traversing the plot, the plot was relocated to avoid the firelane. Within each plot we identified and counted all trees (dbh 10 cm or more at 1.5 m) and saplings (dbh at least 2.5 cm, but less than 10 cm) and visually estimated the cover of honeysuckle and buckthorn.

We sampled the ground layer vegetation using square meter quadrats. One quadrat was placed in each of two adjacent corners of the 200-m^2 plot, for a total of 40 quadrats. The quadrats were offset one meter toward the inside to ensure sampling of undisturbed vegetation. Herb and shrub presence, number of tree seedlings, and estimated cover of honeysuckle and buckthorn were recorded for each quadrat. Sampling took place in early July in each of the four years, starting in 1989.

The east boundary of the forest is the property line between the arboretum and a development of houses on wooded lots. Safety measures to avoid spread of fire beyond arboretum property included reducing the fuel load in the strip of woods along the line by removing downed trunks and branches. To allow movement of the burn crew, all honeysuckle and buckthorn in the strip was cut and treated with herbicide. Prescribed burns were carried out in the remainder of the forest April 16, 1990 and April 17, 1991, while the cut strip was burned April 18, 1991. Temperature was close to 10°C (50°F) for all burns, and relative humidity was 50-55% for the first two burns and 71% for the strip. Wind was SW at 5-12 mph for the 1990 burn and NE at 5 mph for the 1991 burns. Flame heights were 15-30 cm. Approximately 50% of the area burned in the first burn, 60-70% in the second, and 60% in the strip burn. The oak wilt area was particularly difficult to burn because of the lack of oak leaf litter for fuel.

RESULTS

Effect on Trees and Saplings

The number of saplings was substantially reduced by the first burn (Table 1), changed very little after the second burn, and dropped substantially again during the year with no burn. Tree-sized individuals, on the other hand, were reduced in number after each of the two burns, and returned to pre-burn levels after a year of no burn. Basal area per hectare shows a similar pattern, with an ending value of 1449 dm^2 per hectare, just slightly higher than the starting value, even though the site was burned two times in the interim. Compared with a mature dry oak woods in this region, tree and sapling density

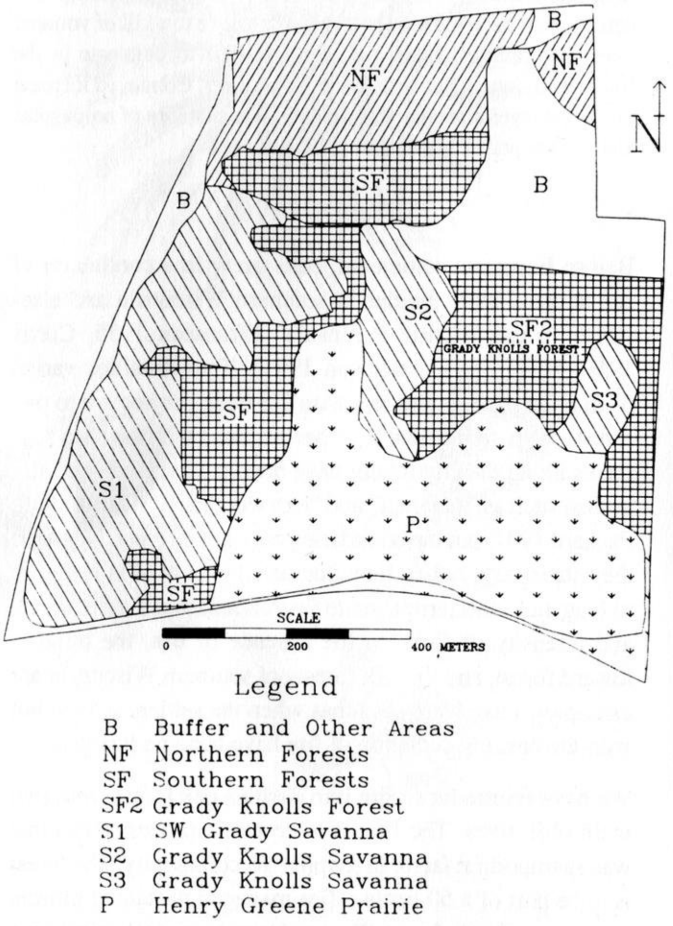

Figure 1. A map showing the location of the study area, Grady Knolls Forest, and other management units in the UW Arboretum Grady Tract.

Table 2. Change in sapling and tree species after burning.

	# Saplings	# Trees	BA(dm^2)/tree	BA(dm^2)/ha	RDo*
Quercus velutina x ellipsoidalis Black Oak					
1989	140	58	6.3	914	64.4 %
1990	81	45	7.4	833	61.3
1991	81	41	7.9	810	60.3
1992	66	44	7.7	847	58.5
Prunus serotina Black Cherry					
1989	83	66	1.5	248	17.5 %
1990	81	64	1.6	256	18.9
1991	85	60	1.8	270	20.1
1992	67	77	1.6	308	21.3
Quercus alba White Oak					
1989	84	22	3.0	165	11.6 %
1990	79	23	3.0	173	12.7
1991	73	23	3.1	178	13.2
1992	67	25	3.1	194	13.4
Quercus macrocarpa Bur Oak					
1989	39	10	2.9	73	5.1 %
1990	31	10	3.0	75	5.5
1991	34	7	3.7	65	4.8
1992	33	8	3.7	74	5.1

*RDo = Relative dominance (BA/ha as a percent of total BA/ha)

are somewhat higher, and mean basal area and basal area per hectare are much lower.

Forty percent of the black oak saplings and 35% of the black oak trees were top-killed by the first burn (Table 2). Small trees were top-killed more frequently than large ones, resulting in an increase in mean tree size. There was a substantial decrease in the number of black cherry saplings in 1992 and a similar gain in the number of trees at the same time. This suggests that some of the missing saplings grew enough to be counted as trees, and were not adequately replaced by seedlings achieving sapling size-- possibly a fire effect. There are more black cherry than black oak individuals, but, because they are small, the total basal area of black cherry is much less than that of black oak. White oak saplings decreased in number slowly, while the trees showed little change in number or size.

Changes in Honeysuckle and Buckthorn Cover

Before the first prescribed burn, the mean cover of honeysuckle and buckthorn in all plots that had not been cut was 85%. The first burn reduced the cover to 56% and the second to 38%. The following year there was a slight increase, to 41%. Most of the individuals resprouted from the base, but the resprouts were not very vigorous. Some completely dead honeysuckles were observed in 1992. This may be the result of fire "girdling" the previous year.

Changes in Ground Layer Diversity

Seventeen species were present in the quadrats in 1989, before the burn. This increased to 42 after the first burn, and to 46 after the second burn. The following year 45 were recorded, essentially no change. Over half of the 45 species were native shrubs (12 species) and herbs (13) that are most often found in forests (Curtis 1959). This group (referred to as "woodland species" in Figure 3) increased every year. Native species most often found in prairies and savannas were not present at the start; 18, including 3 considered very weedy in habit, appeared after the first burn, but only 5 persisted. Exotic herbaceous species increased after each burn; there were 10 species present the final year. (For species lists and a more detailed analysis of the data for the ground layer, see Kline and McClintock, in press.)

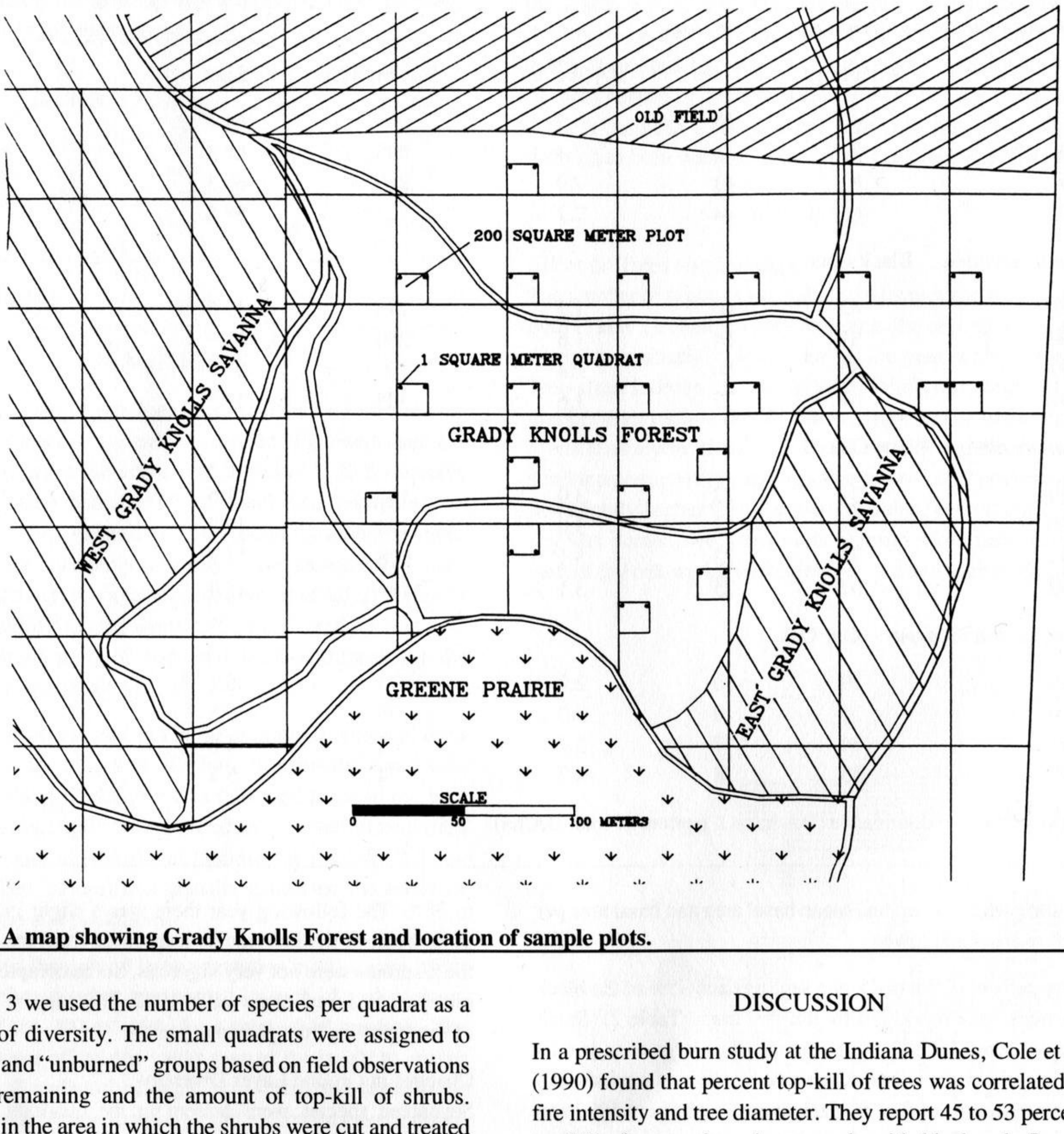

Figure 2. A map showing Grady Knolls Forest and location of sample plots.

In Figure 3 we used the number of species per quadrat as a measure of diversity. The small quadrats were assigned to "burned" and "unburned" groups based on field observations of litter remaining and the amount of top-kill of shrubs. Quadrats in the area in which the shrubs were cut and treated with herbicide were treated as a separate group. This "cut and burn" group was burned only in 1991.

Number of species per quadrat increased in all three quadrat groups, but the increase was greatest in the burned group. The burned plots had the highest values for both prairie and exotic species. Woodland species were more common and increased more than prairie and exotic species in all three groups. The burned quadrats had prairie species present every year after the first burn, but the number of prairie species per quadrat decreased each year. Increases in the cut group were greatest after the burn (1991), and much less the year of the cut (1989).

DISCUSSION

In a prescribed burn study at the Indiana Dunes, Cole et al. (1990) found that percent top-kill of trees was correlated to fire intensity and tree diameter. They report 45 to 53 percent top-kill after one burn in a woods with black oak. In our study, two fires resulted in a 29% top-kill of black oak (most of them small), a 9% top-kill of black cherry, and a 20% top-kill overall. The lower rates suggest a relatively low fire intensity. The difference in top-kill of oak compared with cherry may be due to leaf litter differences, oak leaves supplying better fuel than the small, rapidly decaying leaves of black cherry.

Changes brought about by fire can be slow. Thirteen years of annual prescribed burns in a dry oak woods in central Minnesota have made the woods more open but have not yet reduced tree density to that of a savanna (White 1983). Lorimer (1985) has suggested that fire might be used to enhance oak regeneration in oak forests, but cautions that a

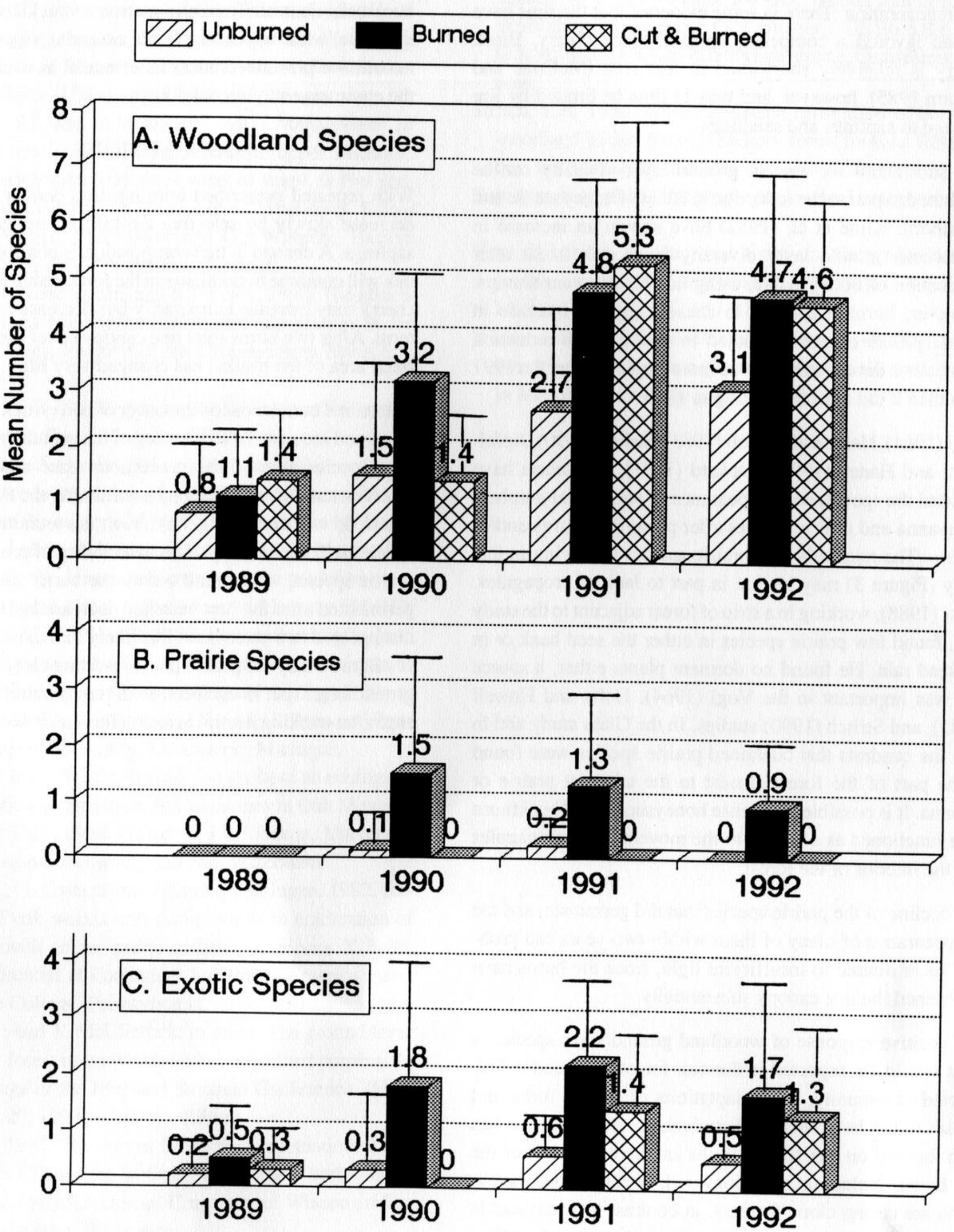

Figure 3. Change in number of ground layer species per square meter quadrat (under three different treatments).

single burn may favor competing species over oaks. There is no evidence in the present study that the two burns improved oak regeneration. There is some evidence that the fires have indeed favored a competing species, black cherry. Black cherry is relatively short-lived in this area (McCune and Cottam 1985), however, and may in time be limited by fire damage to saplings and seedlings.

The substantial increase in ground layer diversity can be attributed in part to the reduction in cover of honeysuckle and buckthorn. Kline et al. (1982) have shown an increase in herbaceous ground layer diversity in an oak forest after eradication of honeysuckle, using herbicide on cut stumps. However, burning appears to cause a greater increase in diversity than can be attributed to exotic shrub reduction alone, since the cut area showed more response after the 1991 burn than it did after the cutting in 1989.

Vogl (1964), Holtz and Howell (1983), Stritch (1990), Apfelbaum and Haney (1991), Packard (1991), and others have reported the spontaneous appearance of substantial numbers of savanna and prairie species after prescribed burns and/or cutting. The relatively few prairie species appearing in this study (Figure 3) may be due in part to lack of propagules. Glass (1988), working in a strip of forest adjacent to the study area, found few prairie species in either the seed bank or in the seed rain. He found no dormant plants either, a source that was important in the Vogl (1964), Holtz and Howell (1983), and Stritch (1990) studies. In the Glass study and in ours the quadrats that contained prairie species were found in the part of the forest closest to the adjacent prairie or savanna. It is possible that dense honeysuckle and buckthorn have functioned as a barrier to the movement of propagules into the interior of the forest.

The decline of the prairie species that did germinate, and the disappearance of many of them within two years can probably be attributed to insufficient light, since the burns have not opened the tree canopy substantially.

The positive response of woodland ground layer species is what would be expected if the oak forest is indeed a fire-adapted community. The adaptations of prairie forbs and grasses to fire have been well studied, but little attention has been focused on oak forest shrubs and herbs. Shrubs of the oak forest, including gray dogwood, hazelnut, and blackberry, are strong clone formers, in contrast to honeysuckle and buckthorn. This is probably very advantageous for effective post-fire resprouting.

It is likely that repeated burns can suppress the woody exotics enough to allow development of a diverse ground layer with enough biomass to help fuel the fires. Eventually, repeated burns may deplete the root reserves of honeysuckle and buckthorn so that resprouting will be the exception. Heidorn (1991) indicates that 5 or 6 annual burns will be required for buckthorn control. Total elimination of buckthorn and honeysuckle, while appealing, is not essential, since the plan is to continue prescribed burns indefinitely, as a natural part of the environment of an oak forest.

CONCLUSIONS

With repeated prescribed burning, tree density is likely to decrease slowly by selective top-kill of younger trees and saplings. A change in tree composition is possible, but black oak will continue to dominate in the foreseeable future. Black cherry may increase temporarily but decrease over the long term. After two burns total tree canopy cover (as reflected in basal area of the trunks) has changed very little.

Prescribed burns reduced the cover of honeysuckle and buckthorn and increased the diversity of the ground layer. Woodland species showed the greatest increase and showed as much increase after the second burn as after the first. Whether this trend will continue is unknown; the recruitment of new species will depend in part on availability of propagules. No prairie species were found before the burns, and those that germinated after the first burn had decreased in frequency or disappeared two years later. It is likely that most of the forest is still too shady for prairie plants. Adding carefully selected ground layer species to increase diversity should be considered after tracking natural invasion for one or two more years.

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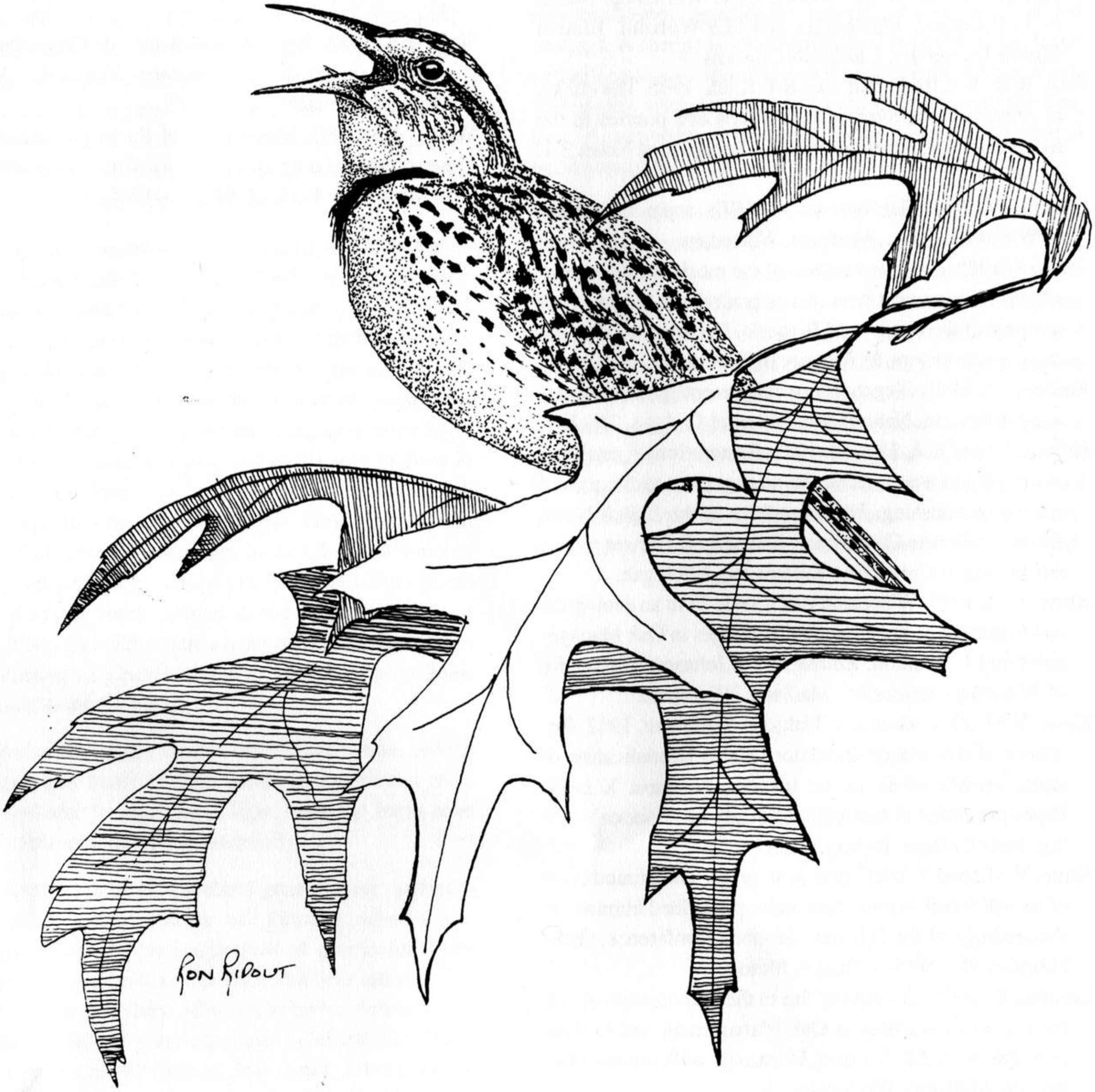
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WATER RELATIONS AND BIOMASS RESPONSES TO IRRIGATION ACROSS A TOPOGRAPHIC GRADIENT IN TALLGRASS PRAIRIE

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Abstract. A long-term study was begun in 1991 to assess the effects of water supplementation along a 100 m transect that spanned upland and lowland annually burned tallgrass prairie on the Konza Prairie in NE Kansas. Irrigation was scheduled to meet predicted evapotranspirational demands. At 12 points along the transect, and in an adjacent control transect, seasonal patterns in plant water status of big bluestem (*Andropogon gerardii* Vitman.) and end-of-season (peak) total aboveground biomass production were measured. In the control transect, greater levels of midday water stress were observed in uplands relative to hillside and lowlands, but irrigation resulted in similar plant water status along the entire topographic gradient. Seasonally, irrigation increased midday leaf water potentials in big bluestem by 42% in uplands, 35% in lowlands and 28% at hillside sites relative to the control transect. Biomass responses were also greatest in the uplands (61%) and least at the hillside sites (45%). This landscape-level experiment is scheduled to run for 10 years to assess long-term effects of water supplementation on site productivity, species composition and soil properties.

INTRODUCTION

In most grasslands, water availability usually limits key ecosystem processes, such as net primary production (NPP), during portions of the growing season. Although the tallgrass prairie lies at the eastern, and most mesic, edge of the extent of North American grasslands, multi-year and seasonal droughts, and their effects on the tallgrass biota, are well-documented (Weaver 1954; Knapp 1984). Relative to other grasslands, tallgrass prairies may experience the greatest year-to-year range in annual precipitation. For example, it is not uncommon for a year characterized by severe drought to be followed by a year in which virtually no water stress is measurable (Knapp 1984). Indeed, because annual precipitation in the tallgrass prairie is sufficient to support more mesic, woody vegetation (Bragg and Hulbert 1976), drought is often included with fire as key factors maintaining these systems as grasslands (Weaver 1954; Knapp and Seastedt 1986; Collins and Wallace 1990).

In the topographically dissected Flint Hills of NE Kansas, it is difficult to assess the degree of limitation to biotic processes caused by water limitation because of two factors: (1) soil types and depth vary significantly with topographic position, and (2) "control" data from sites where other climatic factors are similar, but water is non-limiting, are absent under natural conditions. A core research area of the Long Term Ecological Research (LTER) Program at Konza Prairie is to elucidate controls of NPP and other system characteristics (Callahan 1984). Hence, we established a long term (10 year) irrigation transect in 1991 to assess the role of water as a factor controlling ecological processes across topographic gradients in tallgrass prairie. Below, we describe the study, report results from the first year, and discuss several hypotheses to be tested by this experiment.

METHODS

Research was conducted on the Konza Prairie Research Natural Area (KPRNA) in NE Kansas. KPRNA is a 3,487 ha tract of unplowed, native tallgrass prairie dominated by big bluestem (*Andropogon gerardii)*, Indian grass *(Sorghastrum nutans*) and a variety of forbs (Freeman and Hulbert 1985). In 1991, an irrigation transect was established near the KPRNA headquarters in an annually burned (spring) area. The transect is 100 m in length and spans upland, hillside and lowland topographic positions (Figure 1). A total of twelve 1.5 m tall high-impact sprinkler heads equipped with discharge regulators and supplied by 7.5 cm diameter irrigation pipe were installed at 10 m intervals. A grid of 24 rain gages located along a portion of the transect was used to quantify the amount and distribution of water added by the sprinklers (Figure 1). Maximum application rate along the center of the transect was 8 mm/hr. Distribution of water was non-uniform at the ends of the transect and at a rock outcrop where irrigation was from a single sprinkler head. Each rotating sprinkler head provided water to a radius of 15 m from the transect (Figure 1) and all measurements of tallgrass prairie responses were made within ±3 m of the sprinkler line, where the maximum amount of water was added. An adjacent transect north of the irrigated area was marked and used as a control site.

Irrigation was scheduled to maintain the sum of actual rainfall and supplemental water slightly above estimated actual evapotranspiration (ET) levels. ET was estimated with established Penman combination equations (Lamm et al. 1987) and data from a weather station located <200 m from the transect.

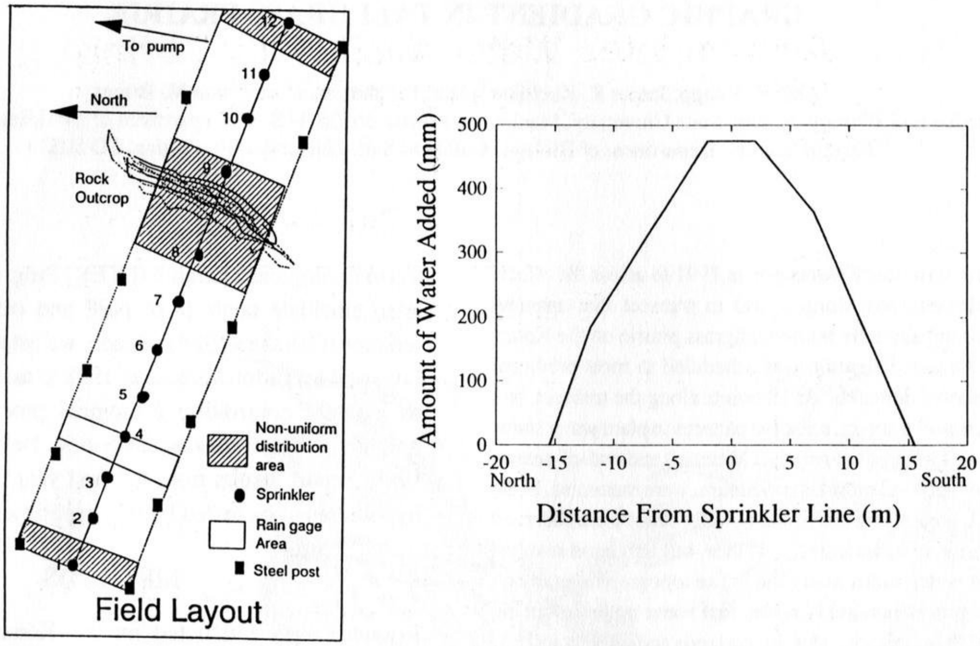

Figure 1. Diagram of irrigation transect (left) with locations of sprinklers numbered. Upland sites are 9-12, hillside sites are 6-8, and lowland sites 1-5. Steel posts delimit the perpendicular extent of water supplied by the sprinklers. Non-uniform distribution areas occur where individual sprinklers do not have adjacent sprinkers on either side. The rain gage area is where a grid of gages is used to quantify the distribution of water added. The amount of water added during the 1991 season within this rain gage area is shown in the right panel. Water reached 15 m on either side of the line of sprinklers (denoted by "0").

Water status of the dominant tallgrass prairie species, big bluestem, was measured at about 2 week intervals throughout the growing season in both the irrigation and the control transect. Water status was assessed by estimating xylem pressure potential (XPP) with a pressure chamber (PMS model 1000) in 5-7 leaves collected at predawn and midday (1300 CST). Predawn values provide an estimate of maximum XPP after plants have equilibrated with soil moisture overnight, and midday values represent the lowest values of XPP occurring during the day. Reductions in XPP below -1.5 MPa reduce physiological activity in big bluestem (Knapp et al., 1993).

Near the end of the growing season (Sept.), aboveground NPP was quantified by harvesting all biomass within 4 0.1 m^2 quadrats randomly placed adjacent to each of the 12 sprinkler locations along the irrigation transect, and at parallel sites in the control transect. Biomass was separated into grass and forb components, oven-dried and weighed to the nearest 0.1 gram.

RESULTS AND DISCUSSION

Almost 500 mm of water was added to the irrigation transect in 1991 (Figure 1). Actual rainfall was substantially below the 30-yr mean for Manhattan, KS (located 12 km north of KPRNA), but 20 irrigation events, each adding about 20 mm of water, resulted in the sum of natural rain plus supplemental water to be in excess of estimated ET (Figure 2). The decision to irrigate was made weekly based on estimates of ET and the previous week's rainfall, thus, irrigation events were not spaced evenly throughout the season. Instead, irrigation occurred most frequently during July and August when rainfall was lowest and temperatures were the highest.

Irrigation appeared to increase the water status (XPP) of big bluestem relative to control plants along the entire topographic gradient (Figure 3). When data from topographically similar sites were combined for the control transect, big bluestem at the upland sites had lower seasonally averaged XPP ($p < 0.05$, ANOVA) compared to hillside and lowland sites for both predawn and midday sampling periods. In contrast, there were no differences among topographic positions in XPP for the irrigated plants. Thus, at predawn, irrigation at the uplands sites resulted in the greatest reduction in potential water stress, with hillside and lowland sites similarly affected (Figure 3). At midday, the smallest difference between irrigated and control XPP occurred at the

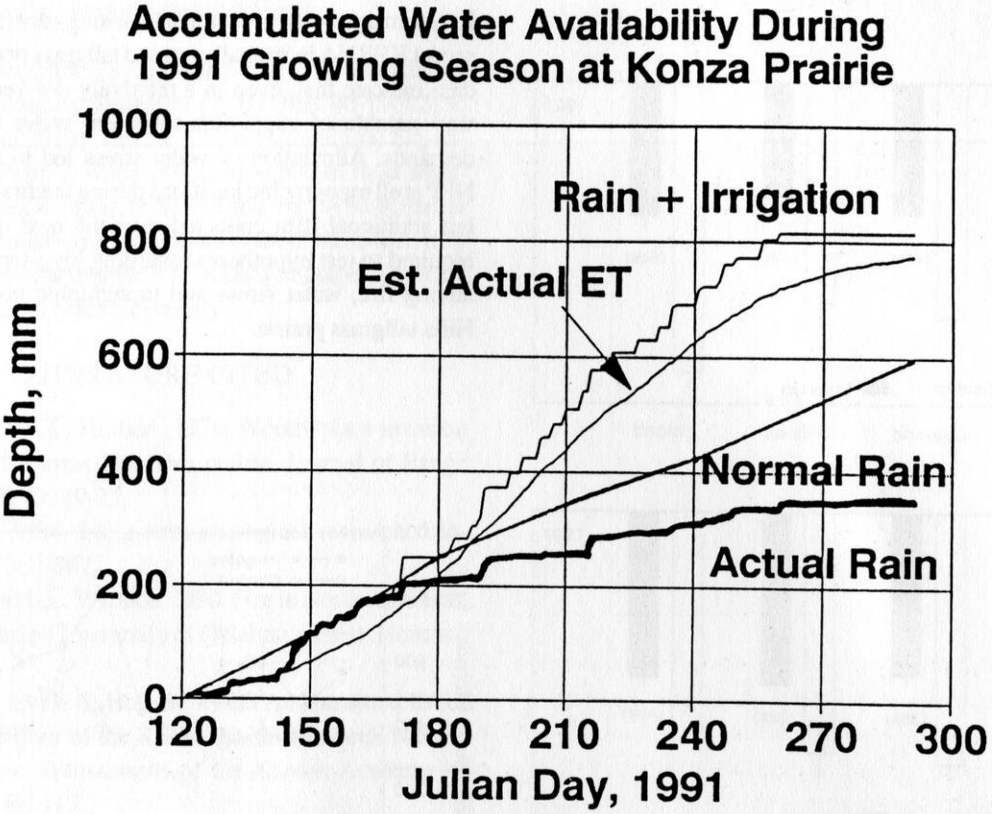

Figure 2. Season course of actual rainfall at headquarters on Konza Prairie (1991), "normal" rainfall (30-yr mean) for Manhattan KS (<15 km from Konza Prairie), estimated actual evapotranspiration (ET) based on weather data from headquarters, and the sum of rainfall plus irrigation water added to the transect.

hillside locations with the greatest difference again at the upland sites (Figure 3). These data show the expected pattern of greater water stress at upland sites with shallow soils (Knapp 1985) but they also suggest that topographic interactions with plant water status may be absent in very wet years.

As expected, supplemental water increased ($p < 0.05$) aboveground biomass production along the irrigation transect relative to adjacent control sites (Figure 4, top). When measurements from topographically similar sites were combined along the control transect, NPP was greater ($p < 0.05$, ANOVA) at the hillside locations relative to the lowland, with the upland sites not different from either the lowland or the hillside sites (Figure 4, bottom). In contrast, no difference in NPP was detected among topographic positions along the irrigation transect, although trends were similar to the control transect. Irrigation resulted in the greatest proportional increase in NPP at upland and lowland sites relative to control data, with the smallest increase at hillside locations (Figure 4, bottom).

These patterns in NPP in response to irrigation are consistent with estimates of midday XPP (Figure 3). The hillside sites (6, 7 and 8) occurred below a rock outcrop (Figure 1). Such outcrops typically result in intermittent "seeps" caused by the downward flow of soil water being deflected by relatively impermeable limestone strata. Moreover, the finer textured soils in the lowlands apparently had lower infiltration rates relative to the uplands sites (inferred from the presence of standing water at lowland sites) and this may have led to reduced differences in XPP and NPP between uplands and lowlands than might have been expected. The lack of differences in NPP among topographic locations along the irrigation transect supports the view that all sites may be equally productive given similar water availability.

Additional Goals Of The Irrigation Experiment

Although estimates of NPP and plant water status will continue to be made during the scheduled 10-year duration of this experiment, replicate irrigated and control transects will be established in 1993 to allow for more robust statistical analysis of the data. Along these transects, a number of other variables will be measured to address additional hypotheses. Soil moisture in irrigated and control sites measured using a time domain reflectometry system and an array of probes is scheduled to begin in 1993. This will enable us to better characterize differences in water availability across topo-

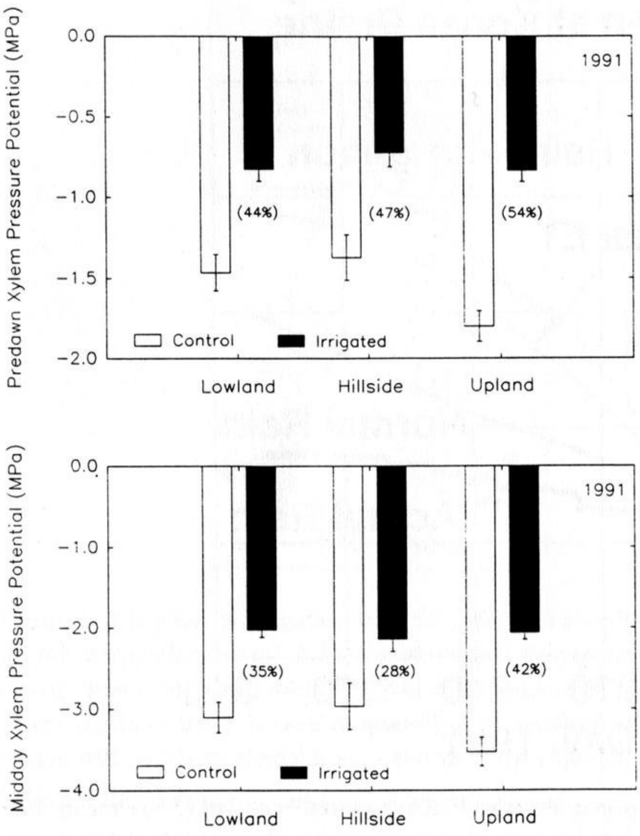

Figure 3. Comparison of seasonally averaged predawn and midday xylem pressure potential measurements for big bluestem at three topographic positions along the irrigated and control transects. Numbers in () indicate the per cent difference between irrigated and control values. Vertical bars represent ± 1 standard error of the mean. Lowland (1-5), hillside (6-8) and upland (9-12) sites refer to locations in Fig. 1.

graphic gradients. Vegetative species composition was quantified in 1991 and will be reassessed annually along the irrigated and control transects to test the hypothesis that annual spring fires are sufficient to maintain the grasses dominant even if water is not limiting. Soil organic matter and nutrient content was also measured initially and will be measured again at the conclusion of the study. These data, along with annual measures of site productivity, will be used to test hypotheses regarding the effect of long-term annual burning on soil fertility. Results from simulation models predict that soil C, N and ultimately NPP will be reduced under an annual burning regime (Ojima et al. 1990). The long term addition of supplemental water to annually burned tallgrass prairie may accelerate these changes.

In summary, we have established a long-term irrigation transect at KPRNA in annually burned tallgrass prairie. First year data indicate that, even in a relatively dry year, our system was capable of supplying sufficient water to exceed ET demands. Alleviation of water stress led to an increase in NPP at all topographic locations during the first year of study, but additional data collected over the next decade will be required to test hypotheses regarding long-term interactions among fire, water stress and topographic position in Flint Hills tallgrass prairie.

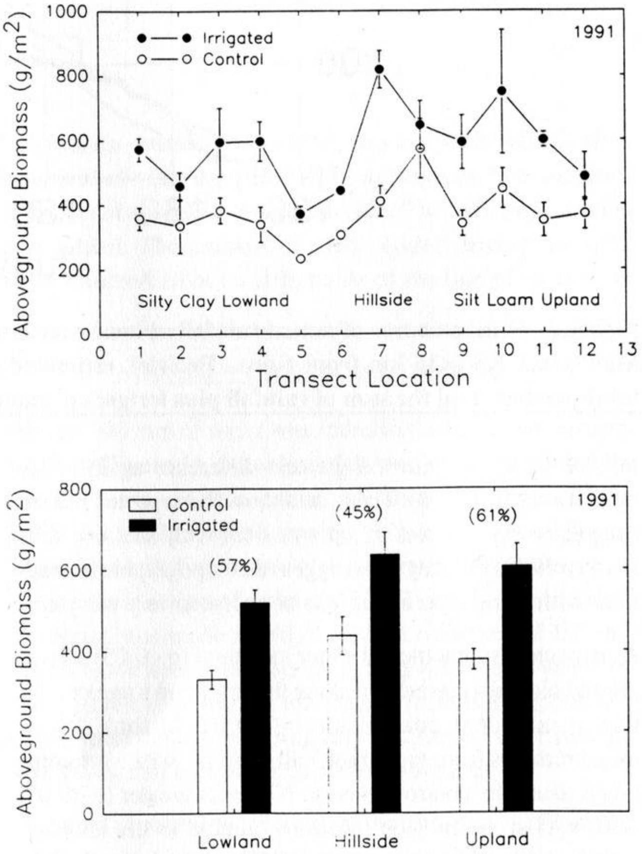

Figure 4. Top: Variation in aboveground biomass (an estimate of NPP) along the irrigation and control transects in 1991. Transect location numbers correspond to the sprinkler numbers in Figure 1. Vertical bars denote ±1 standard error of the mean. Bottom: Comparison of aboveground biomass in irrigated and control transects according to topographic positions (see Figure 3). Numbers in () indicate the per cent differences between irrigated and control values. Vertical bars denote ±1 standard error of the mean.

ACKNOWLEDGEMENTS

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SEED BANKS OF COMMUNITIES IN THE IOWA LOESS HILLS: ECOLOGY AND POTENTIAL CONTRIBUTION TO RESTORATION OF NATIVE GRASSLAND

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Abstract. Species compositions' of the seed banks associated with native grassland, exotic grassland, and woody communities from two sites on the Loess Hills landscape in west central Iowa were determined by greenhouse germination trials. A total of 87 species was identified in the seed banks of the communities at both sites. Fourteen species, mostly perennials of disturbed habitats, had seed densities greater than 100 seeds/m^2.

Qualitative similarity between the compositions of the seed banks at the two sites was high, probably because of similarities in the past and present vegetation on the sites. Although both sites were previously grazed, the site more recently grazed had a higher qualitative similarity between the seed bank and the vegetation and had a lower total seed density. Very little similarity was observed between the seed bank and present vegetation of the communities. Total seed density decreased along a gradient from the woodland communities (lowest elevation) to the mid-grass communities (highest elevation), which also represented a gradient of increasing environmental stress.

Twenty-nine native plant species of extant Loess Hills grassland were observed in the seed banks of deciduous and coniferous woodland, deciduous shrubland, and exotic grassland. However, when a seed bank species's inherent value for restoration was considered, the seed banks had limited potential for contributing to the restoration of native grassland. Especially indicative of the low potential was the seed bank of the woodland communities, which contained only four species with significant value.

INTRODUCTION

In western Iowa, adjacent to the Missouri River floodplain, is a narrow band of rugged hills formed by deposition of loess during the last 20,000 years of the Pleistocene (Prior 1991, Figure 1). Prior to Euro-American settlement in the 1830's, the Loess Hills landscape was apparently dominated by native grassland, with very little woodland (Brackenridge 1816, Bell 1820, Maximillian 1833). Today, much of the Loess Hills is dominated by early successional woody vegetation (Heineman 1982), most likely because of the combined effects of the cessation of grassland fire and the introduction of woody species on farmsteads. The establishment of grassland dominated by exotic grasses on low slope positions (for use as cool-season pastures) has also displaced native grasslands. Native grasslands still exist primarily on upper slope and ridge top positions, where soil moisture levels are presumably less suitable for establishment and growth of woody plants, and where steep slopes prevent access with machinery for conversion to exotic grasses (Figure 2). The juxtaposition of these extant grassland communities with early successional woody communities and exotic grasslands (both in areas formerly occupied by native grassland) provides an excellent setting for investigation of the potential for the restoration of native grassland from remnant seed sources.

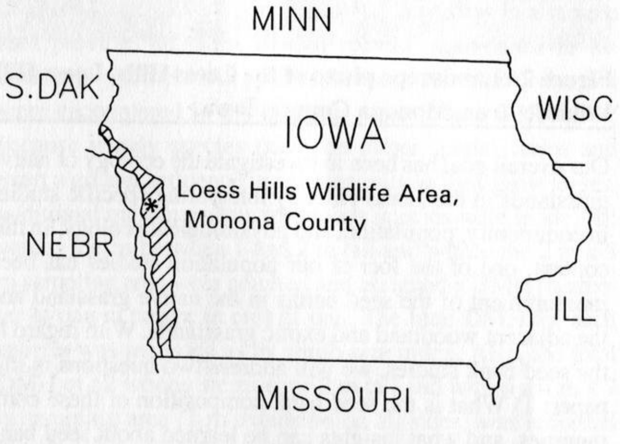


Figure 1. Location of the Loess Hills landform in western Iowa, and the study area in Monona County, Iowa.

The production of seeds that become incorporated into a buried population, or seed bank, is a common feature of many types of vegetation (Fenner 1985, Silvertown 1982, Roberts 1981, Harper 1977). The primary ecological importance of the seed bank is the potential contribution it may make to the vegetation through seed germination. Observation of the seed bank may provide some ability to predict what plant species may become established if conditions are such that the germination of seeds is favored. Vegetation theory (Glenn-Lewin et al. 1992, Grubb 1988, Pickett and White 1985) and empirical evidence (Goldberg and Werner 1983, Gross and Werner 1982, Gross 1980, Miles 1972) suggest that disturbance to the vegetation (defined here as an event, natural or man-made, that kills or removes individuals in a patch) nearly always initiates a pulse of seed germination. Therefore the seed bank is an integral factor in determining the potential vegetation of a site.

Figure 2. Landscape photo of the Loess Hills, Loess Hills Wildlife Area, Monona County, Iowa.

Our overall goal has been to investigate the ecology of native grasslands in the Loess Hills by integrating specific studies in community, population, and physiological ecology. In this context, one of the foci of our population studies has been measurement of the seed banks in the native grassland and the adjacent woodland and exotic grasslands. With regard to the seed bank studies, we will address two questions in this paper: 1) What is the seed bank composition of these communities, and what insights can be learned about seed bank ecology? 2) In habitats that formerly were native grassland, but are presently occupied by postsettlement communities that are not native grassland, is there any potential for natural regeneration (i.e., restoration) of native grassland species from the seed banks?

Since the first prairie restoration work began in the 1930's at Curtis Prairie in Madison, Wisconsin and at Homestead National Monument near Beatrice, Nebraska, interest and knowledge in prairie restoration have continued to expand. Regeneration of native vegetation on a site devoid of any remnant prairie vegetation, such as an agricultural field, must depend completely on seeding or transplanting techniques. On the other hand, a pasture containing remnant prairie plants within a sward of exotic cool-season grasses presents a much different starting point and requires a different methodology (Rosburg and Glenn-Lewin 1992). To help differentiate these ends of what is essentially a continuum, the use of the word reconstruction in situations heavily dependent on seeding or transplanting helps convey the sense of rebuilding from anew, while restoration can be applied to situations that at least start with ecological information (i.e., remnant plants or seeds), to help convey the sense of reviving and invigorating the remnant components. This paper uses the word restoration in that sense.

METHODS

Field Research

Seed bank and vegetation measurements were made at two sites (hereafter referred to as sites 1 and 7) in the Loess Hills Wildlife Area (LHWA), Monona County, Iowa (Figure 1). The LHWA is a state-owned wildlife management area that contains some of the largest and most pristine native grassland remaining in the Loess Hills (Figure 2.). Fire management was initiated by the state soon after land acquisition occurred in 1972 for site 1, and in 1980 for site 7. In 1990, we made seed bank and vegetation measurements at 5 m intervals along a 110 m transect at site 1. The transect was located perpendicular to a ridge, with 50 m extending down from the ridgetop on a south-facing aspect and 60 m extending down the opposite north-facing aspect. In 1991, the same methodology was applied to site 7, except that here three aspects were present. Thus the transect was three-pronged with the center on the peak common to all three aspects. The transect at site 7 ran 55 m down an east-facing aspect, 40 m down a northwest-facing aspect, and 40 m down a southwest to south-facing aspect (Figure 3).

Seed bank

We measured the seed bank by collecting soil samples (i.e., seed bank samples) and determining the presence of seeds by germinating them. Therefore we only counted viable seeds of those species whose germination requirements were met by conditions in the greenhouse. No attempt was made to identify seeds by sieving the soil. Seed bank samples were collected in late March 1990 at site 1. At site 7 samples were collected in late March 1991, with two additional samples collected in early March 1992. Early spring sampling allowed natural stratification of seeds to occur over the winter and timed the collections to when seeds would most likely be coming out of dormancy naturally.

For collection of seed bank samples, sample areas of 2 m x 5 m were established at 5 m intervals, with the long dimension perpendicular to the slope, along the transects beginning at the top of the ridge or peak and continuing down the adjacent aspects. Each of these sample areas defines an individual community sample. A stratified random sampling design that divided each sample area into ten 1 m^2 cells was used to collect seed bank subsamples from the sample areas. Two soil cores, each 6 cm in diameter and 5-6 cm deep, were randomly selected from each of the ten cells (Figure 4). The 20 soil cores were divided into upper and lower halves, and the respective halves were pooled to yield two samples, an upper seed bank sample and a lower seed bank sample, from each sample area. Bigwood and Inouye (1988) found that seeds have a generally clustered distribution in the soil, and therefore they suggested that precision in seed bank sampling

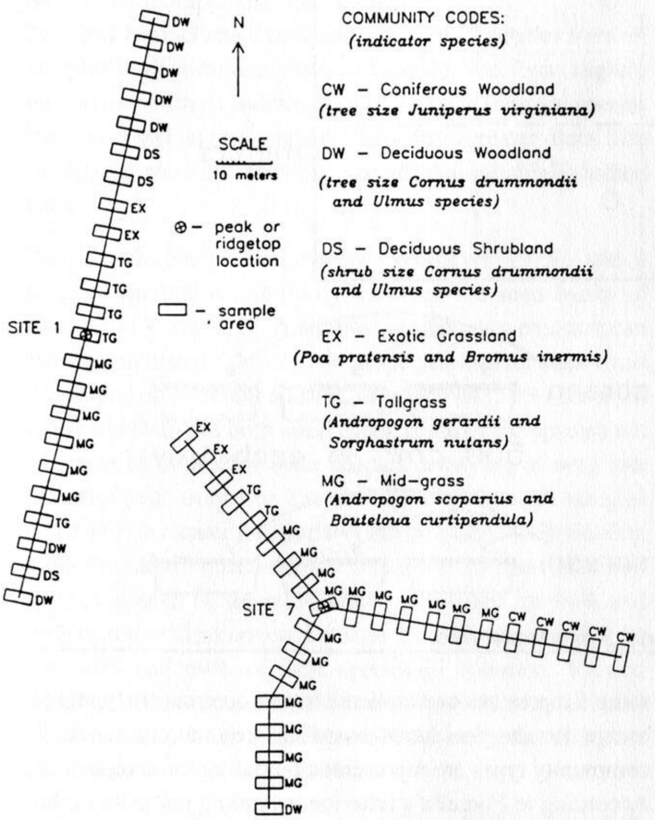


Figure 3. Scale drawing of the transects and sample areas at sites 1 and 7, and identification of the plant communities associated with the sample areas.

can be improved by subsampling large units with very small subunits.

The soil was passed through a screen to remove vegetative propagules, such as roots and rhizomes. From each of the seed bank samples three replicates were established, each consisting of 500 cm^3 of seed bank soil spread in a thin layer over sterilized potting soil in 19 cm x 19 cm trays. Together the three replicate trays contained, on average, 96% of the soil volume in each seed bank sample. The trays were placed in a randomized block design on a table in the Richard Pohl Conservatory Greenhouse at Iowa State University. They were watered as needed, when the soil on the surface showed signs of dryness. After seeds germinated in the trays, species were identified, counted, and the seedlings removed to prevent overcrowding. Examples of each species of seedling were grown to a size adequate for positive identification. Seed bank samples were allowed four months to germinate seeds, from mid-April to mid-August. The total number of seedlings observed in all three replicates is an estimate of the minimum number of viable seeds present in the sample.

Vegetation

Vegetation measurements were made during June along the same transects used for the seed bank collections in 2 m x 5 m samples areas that very nearly corresponded to the sample areas used in collecting the seed bank samples. From each of the ten 1 m^2 cells in a sample area, one 50 cm x 50 cm quarter section was randomly selected. Each of these ten quarter sections was further divided into four 25 cm x 25 cm quadrats. Vegetation measurements were made in each of these forty quadrats using categorical indices (Figure 5). The sum of these indices for all observations of a species in a sample area provides an index of that species' abundance in the community sample. All species, herbaceous and woody, that were encountered in the quadrats were indexed. However, because woody species occur on larger spatial scales and exert a greater influence in a community as they grow larger, additional measurements for woody species were made. All woody stems between 1 and 2 m tall and within the 2 m x 5 m sampling area were counted and assigned a DMH (diameter at one m height in cm) of one. The total DMH for each species was recorded as its shrub-size index. Also, the total DMH of all woody stems over 2 m tall and within a 4 m x 7 m sampling area (1 m extension on all sides) was recorded for all species as its tree-size index. These structural measurements indicate the relative length of time woody vegetation has occupied a habitat. Nomenclature follows Great Plains Flora Association (1986).

Analysis

The seed bank data from both the upper and lower samples in a sample area (six trays) were pooled to yield a single estimate of the number of seeds of each species in the top 6 cm of seed bank within each sample area. Then these data, each representing one observation of the seed bank community associated with a given vegetation, were averaged over all the sample areas in a community type to derive a measurement of the seed bank associated with the present vegetation.

The vegetation measurements were used to identify the community from which the seed bank samples were collected. Visual observation of the vegetation at both sites 1 and 7 suggested that there were six physiognomic community types present. The mid-grass and tallgrass types are native grassland communities. The other four types were exotic grassland, deciduous shrub (shrub signifies woody vegetation that was mostly 1 to 2 m tall), deciduous woodland (woodland signifies woody vegetation that was mostly over 2 m tall), and coniferous woodland; these four types represent communities that potentially could be restored to native grassland. Community samples were objectively assigned to one of these community types by calculating the relative

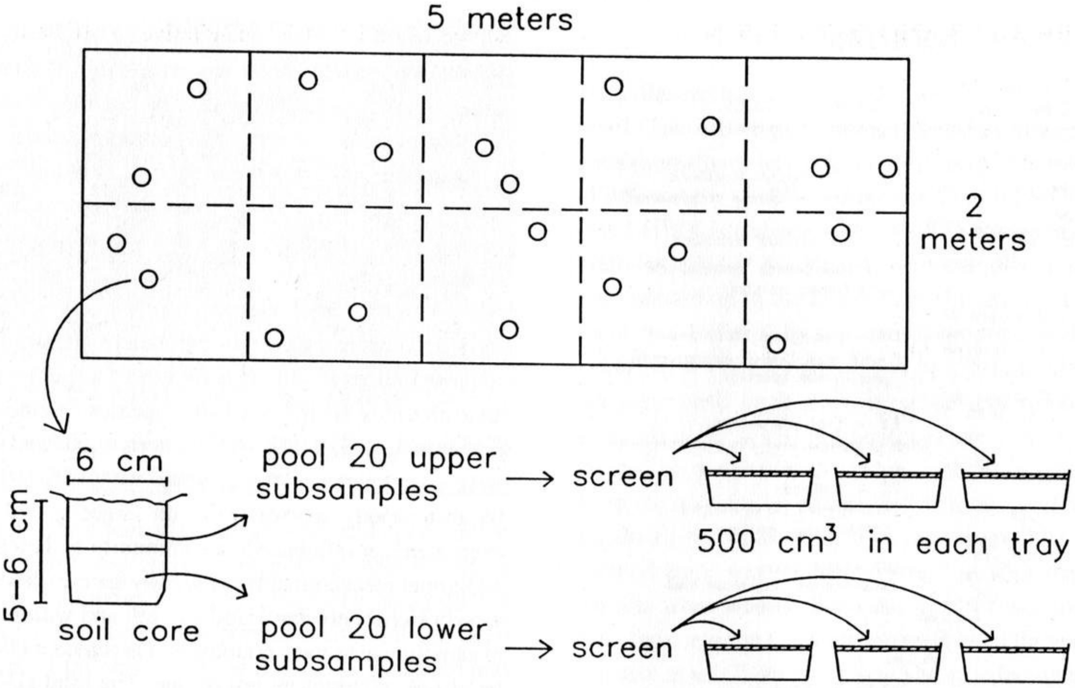
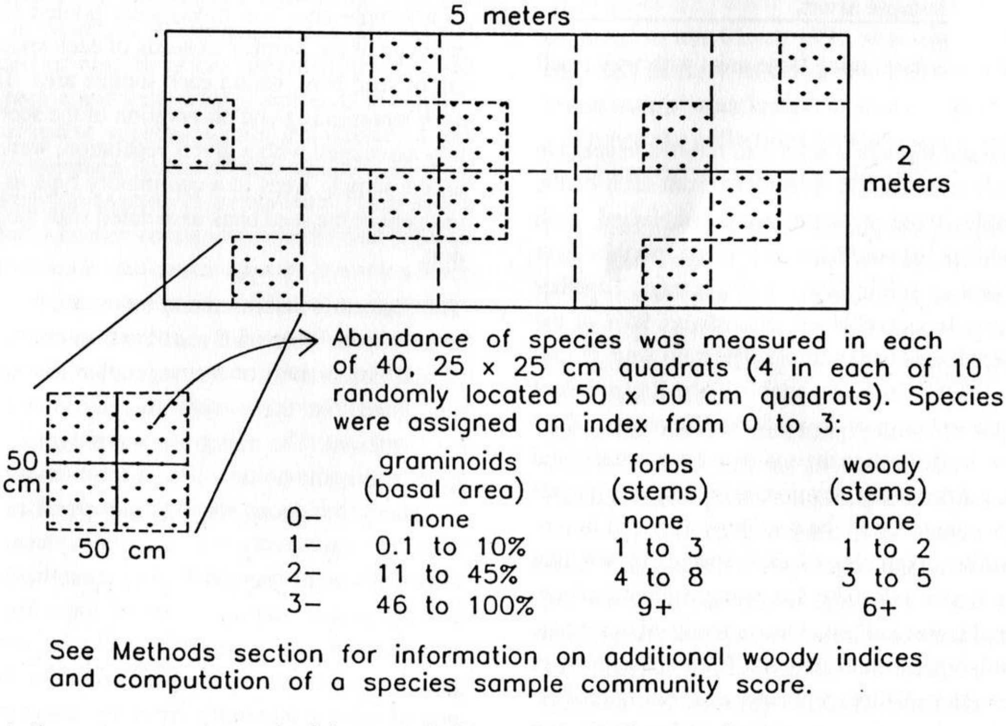


Figure 4. Seed bank sampling methodology applied to each 2 m x 5 m sample area.

abundance of "indicator" species in the samples from their index scores (Figure 3).

Forcella (1984) found that to ascertain differences in the seed bank among treatments in a cultivated grassland, the combined surface area of replicate samples from any one treatment should be 1000 cm^2. In this study, the combined surface area from all subsamples in one sample area is 565 cm^2. Each sample represents one replicate from a community type, and except for the deciduous woodland community at site 7, community types are represented by two or more replicates. According to Forcella's criterion, sampling intensity in this study should be adequate to identify differences in seed banks among communities.



Abundance of species was measured in each of 40, 25 x 25 cm quadrats (4 in each of 10 randomly located 50 x 50 cm quadrats). Species were assigned an index from 0 to 3:

	graminoids (basal area)	forbs (stems)	woody (stems)
0–	none	none	none
1–	0.1 to 10%	1 to 3	1 to 2
2–	11 to 45%	4 to 8	3 to 5
3–	46 to 100%	9+	6+

See Methods section for information on additional woody indices and computation of a species sample community score.

Figure 5. Vegetation measurement methodology applied to each 2 m x 5 m sample area.

RESULTS AND DISCUSSION

Seed Bank Composition and Variation

The seed bank of site 1 included a total of 70 species from all samples in all community types (Table 1). Site 7 was slightly less diverse with 61 species (Table 2). Of the fourteen species that occurred at the highest densities (greater than 100 seeds/m^2), most are perennial species that inhabit disturbed sites.

The Coefficient of Community (Whittaker 1975), which assesses qualitative similarity, between the seed banks of sites 1 and 7 was 67%. A simple commonality measure can also be calculated. The combined species lists for sites 1 and 7 included 87 different species, of which 44 (51%) occurred in the seed bank at both sites. Since some of the species not common to both sites were species occurring at very low densities (e.g., only 1 or 2 seeds recovered from all samples at the site), a clearer comparison can be made by eliminating these "random" observations. Using the 30 most common species at each of the sites, which accounted for 91% and 94% of the seeds recovered at sites 1 and 7 respectively, the two sites had 69% of their species in common. Viewed together, these measures indicate a fairly high qualitative similarity, i.e., a high proportion of the species was observed in the seed banks at both sites.

Percentage Similarity (Whittaker 1975), which is a quantitative measure of similarity, between the seed banks at sites 1 and 7 was 44.6%. Thus there was a decline in calculated similarity when the abundances of species were considered.

Overall, the seed banks at sites 1 and 7 appear to be fairly similar, especially qualitatively. This is, in part, due to the fact that the seed bank of a site is largely a product of the past and present vegetation on the site. Since the sites have similar physical environments and histories (they are only 0.5 km apart), the vegetation at both sites is represented by similar community types and one might therefore expect similarity in the seed banks. For instance, two semiarid grassland sites in Colorado with similar climatic conditions and plant community composition, but different soil texture, also had similar seed bank compositions (Coffin and Lauenroth 1989).

While the qualitative similarity between sites 1 and 7 is most likely a result of their general homogeneity in physical environment and history, which is manifest in a general homogeneity in vegetation between sites, one likely reason for the lack of an equally similar quantitative comparison is the unequal proportions of communities at both sites. For example there were 6 samples of mid-grass vegetation at site 1 and 17 samples at site 7, and 7 samples of deciduous woodland at site 1 but only 1 sample at site 7. If Percentage Similarity were calculated on a community by community basis, this source of variation in quantitative dissimilarity would be removed.

Another useful comparison, especially with respect to site history, is the similarity between seed bank and vegetation. At site 1, 56% of the species observed in the seed bank were also observed in the vegetation, while at site 7, 69% of the species were also observed in the vegetation. Templeton and Levin (1979) suggested that the seed bank of a plant community represents the "memory" of previous conditions. This implies that at site 7 the "previous condition" occurred more recently because the seed bank and the vegetation were more similar. The "memory" Templeton and Levin refer to is the long viability some species have in the seed bank.

Both sites 1 and 7 were grazed, likely for a long period, before they were acquired by the state. We would expect that, since acquisition, the vegetation on both sites has been changing in response to the removal of grazing and the implementation of fire management. Site 1, which was acquired 8 years before site 7 and which also apparently had less grazing pressure (Bob Dolan, Iowa Department of Natural Resources, personal communication), has had more time to either lose certain species from the initial vegetation or gain new species, and thereby become more different from the seed bank, providing the seed bank has species persisting from the previously grazed vegetation. Our observations concur with this history of land use, since the difference between seed bank and present vegetation was greatest at site 1. Indeed, seven of the ten most common species observed only in the seed bank at site 1, hoary vervain (*Verbena stricta* Vent.), yellow wood sorrel (*Oxalis stricta* L.), sand dropseed (*Sporobolus cryptandrus*), horse-weed (*Conyza canadensis* (L.) Cronq.), poverty grass (*Sporobolus neglectus* Nash), black nightshade (*Solanum ptycanthum* Dun. ex DC.), and evening primrose (*Oenothera biennis*), are species that were likely in the vegetation during grazing. Persistent seed bank species and a relatively recent time frame are important elements in this concept. Eventually, even the most persistent seeds die, and if the vegetation supplying seed rain to the seed bank remains fairly stable, the differences between the seed bank and vegetation then may begin to diminish over time.

The number of seeds recovered provides a total seed density measurement for the entire site. At site 1, 1455 seeds were recovered in 23 samples (1160/m^2), while at site 7, 1100 seeds were recovered from 28 samples (720/m^2). This large difference could be due in part to the history of land use between sites. During the more recent period of heavy grazing at site 7, there was likely little opportunity for most plants to become reproductive and contribute seed to the seed bank, thereby promoting lower seed densities.

Table 1. Occurrence of species in seed bank samples at site 1. Total = Number of seeds recovered from all samples at the site; DW = Deciduous Woodland community (7 samples); DS = Deciduous Shrub community (3 samples); EX = Exotic Grassland community (2 samples); TG = Tallgrass community (5 samples); MG = Mid-grass community (6 samples). The superscript (*) indicates species not observed in the vegetation at the site. Underlined densities indicate species that are among the nine or ten most abundant within each community.

		Mean Seed Density (seeds/m^2) Among Community Types				
SPECIES	TOTAL	DW	DS	EX	TG	MG
*_Verbena stricta_	312	165.0	195.5	302.5	506.0	140.5
Poa pratensis	134	47.1	342.2	476.6	29.3	0.0
Sporobolus asper	125	2.6	0.0	91.7	80.7	281.1
Eupatorium rugosum	78	193.8	12.2	9.2	3.7	0.0
*_Conyza canadensis_	65	86.4	48.9	9.2	47.7	30.6
Amorpha canescens	57	0.0	0.0	64.2	29.3	128.3
*_Sporobolus cryptandrus_	57	104.8	55.0	18.3	7.3	12.2
*_Oxalis stricta_ (at least 50 for TOTAL, contaminated with greenhouse _Oxalis corniculatus_)						
Nepeta cataria	50	120.5	24.4	0.0	0.0	0.0
*_Parietaria pensylvanica_	44	102.1	30.6	0.0	0.0	0.0
Muhlenbergia racemosa	38	28.8	97.8	45.8	18.3	3.1
*_Solanum ptycanthum_	30	65.5	6.1	0.0	11.0	3.1
Rubus species	28	70.7	0.0	0.0	0.0	3.1
[1]_Fragaria virginiana_	24	31.4	36.7	0.0	18.3	3.1
*_Sporobolus neglectus_	22	5.2	61.1	0.0	33.0	3.1
*_Oenothera biennis_	21	15.7	24.4	27.5	14.7	12.2
Ceanothus herbaceous	19	0.0	0.0	64.2	44.0	0.0
Teucrium canadense	19	44.5	12.2	0.0	0.0	0.0
*_Typha_ species	18	31.4	12.2	0.0	7.3	6.1
Bouteloua curtipendula	17	0.0	6.1	36.7	11.0	27.5
Heuchera richardsonii	17	0.0	12.2	119.2	7.3	0.0
*_Geum canadense_	16	23.6	42.8	0.0	0.0	0.0
Anemone cylindrica	15	7.9	42.8	36.7	3.7	0.0
Dichanthelium oligosanthes	15	2.6	6.1	27.5	29.3	6.1
Carex blanda	13	28.8	12.2	0.0	0.0	0.0
Sorghastrum nutans	13	2.6	36.7	55.0	0.0	0.0
*_Euphorbia glyptosperma_	12	13.1	6.1	0.0	11.0	9.2
*_Panicum capillare_	12	7.9	24.4	0.0	14.7	3.1
Ambrosia psilostachya	10	15.7	24.4	0.0	0.0	0.0
Medicago lupulina	8	15.7	0.0	18.3	0.0	0.0
Morus alba	8	18.3	0.0	0.0	3.7	0.0
Solidago rigida	8	0.0	0.0	0.0	3.7	21.4
Viola pratincola	8	18.3	6.1	0.0	0.0	0.0
Erigeron strigosus	7	0.0	18.3	0.0	3.7	9.2
Viola sororia	7	18.3	0.0	0.0	0.0	0.0
Chenopodium album	5	10.5	6.1	0.0	0.0	0.0
*_Dichanthelium acuminatum_	5	2.6	18.3	0.0	3.7	0.0
*_Physalis longifolia_	5	7.9	0.0	0.0	3.7	3.1
Rhus glabra	5	10.5	0.0	0.0	0.0	3.1
*_Hedeoma hispidum_	4	5.2	0.0	0.0	7.3	0.0
*_Polygala verticillata_	4	5.2	6.1	0.0	0.0	3.1
Ulmus species	4	0.0	6.1	18.3	0.0	3.1

Table 1. continued

Aster ericoides	3	0.0	0.0	18.3	3.7	0.0
Cornus drummondii	3	5.2	6.1	0.0	0.0	0.0
**Muhlenbergia schreberi*	3	7.9	0.0	0.0	0.0	0.0
Solidago canadensis	3	0.0	6.1	0.0	3.7	3.1
**Urtica dioica*	3	7.9	0.0	0.0	0.0	0.0
**Verbena urticifolia*	3	2.6	6.1	9.2	0.0	0.0
**Veronica peregrina*	3	5.2	0.0	0.0	0.0	3.1
Viola pedatifida	3	0.0	6.1	9.2	3.7	0.0
Aster laevis	2	0.0	6.1	0.0	3.7	0.0
Muhlenbergia cuspidata	2	0.0	0.0	0.0	0.0	6.1
**Plantago rugelii*	2	5.2	0.0	0.0	0.0	0.0
Sisyrinchium campestre	2	0.0	6.1	0.0	3.7	0.0
Andropogon gerardii	1	0.0	0.0	0.0	3.7	0.0
Andropogon scoparius	1	0.0	0.0	0.0	0.0	3.1
**Asclepias syriaca*	1	2.6	0.0	0.0	0.0	0.0
**Dalea candida*	1	0.0	0.0	0.0	3.7	0.0
**Eragrostis minor*	1	2.6	0.0	0.0	0.0	0.0
**Euphorbia dentata*	1	0.0	0.0	0.0	3.7	0.0
Gaura coccinea	1	0.0	0.0	0.0	0.0	3.1
**Lactuca serriola*	1	0.0	0.0	0.0	3.7	0.0
**Linum sulcatum*	1	0.0	0.0	0.0	3.7	0.0
Sanicula species	1	2.6	0.0	0.0	0.0	0.0
**Setaria viridis*	1	0.0	0.0	0.0	0.0	3.1
Solidago speciosa	1	0.0	0.0	0.0	0.0	3.1
**Verbascum thapsus*	1	2.6	0.0	0.0	0.0	0.0
**Verbena bracteata*	1	2.6	0.0	0.0	0.0	0.0
Vitis species	1	2.6	0.0	0.0	0.0	0.0
Totals	1455	1356.6	1216.0	1338.2	978.9	739.4

[1] Includes an undetermined number of *Potentilla norvegica* seeds.

Also, over half of the samples at site 7 were in the mid-grass community, which is the vegetation that occupies the most xeric environments in the Loess Hills, while only a fourth of the samples at site 1 were from mid-grassland. Reduced seed densities in the mid-grassland may arise for two reasons. The first is that seed production in this community could be lower due to the xeric nature of the environment, thereby decreasing the on-site seed rain into the seed bank. Second, seed lying in the soil under the mid-grassland could be subject to a less favorable environment for maintenance of seed viability. A general tenet is that the cooler and drier the storage environment, the longer orthodox seeds (seeds adapted to desiccation) retain viability (Priestly 1986). Certainly the relatively higher soil temperatures associated with the more xeric mid-grassland could be detrimental to seed persistence. Furthermore, when some seeds are stored in excessively dry conditions, their rate of deterioration may increase (Priestly 1986). The reason why the mid-grass community is so common at site 7 is not completely certain, but the more recent history of overgrazing, and perhaps low fertility levels that might result from the over harvest of forage, could be important.

The presence of many viable seeds of cat-tail (*Typha* sp.) in the samples from both sites provides striking evidence of this species' great potential for long distance wind dispersal. Although the source of the cat-tail seed is not certain, no habitat suitable for cat-tails exists within at least 0.7 km from the seed bank sites. Considering the limited occurrence of marsh habitat in the Loess Hills, there is a high probability that the dispersal distance may be over 1 km.

Community-Level Patterns

Variation in total seed density among communities is evident in Tables 1 and 2. A similar pattern can be seen at both sites, with total seed density decreasing along a gradient from woodland to mid-grassland (i.e., with increasing elevation in the landscape, Figure 3). Thompson (1978) suggested that

Table 2. Occurrence of species in seed bank samples at site 7. TOTAL = Number of seeds recovered from all samples at the site; CW = Coniferous Woodland community (5 samples); DW = Deciduous Woodland community (1 sample); EX = Exotic Grassland community (3 samples); TG = Tallgrass community (2 samples); MG = Mid-grass community (17 samples). The superscript (*) indicates species not observed in the vegetation at the site. Underlined densities indicate species that are among the nine or ten most abundant within each community.

		Mean Seed Density (seeds/m^2) Among Community Types				
SPECIES	TOTAL	CW	DW	EX	TG	MG
Verbena stricta	241	146.7	183.3	201.6	302.5	134.8
**Verbascum thapsus*	90	216.3	18.3	177.2	9.2	0.0
Oxalis stricta	77	77.0	18.3	293.3	18.3	5.4
Sporobolus cryptandrus	71	58.7	73.3	18.3	9.2	50.7
Euphorbia glyptosperma	64	29.3	0.0	61.1	91.7	38.8
Carex brevior	58	3.7	0.0	18.3	9.2	57.2
Dichanthelium oligosanthes	56	25.7	0.0	122.2	119.2	17.3
**Sporobolus neglectus*	53	117.3	0.0	12.2	36.7	16.2
Erigeron strigosus	46	29.3	0.0	6.1	0.0	39.9
**Sphenopholis obtusata*	31	18.3	311.6	0.0	0.0	9.7
Euphorbia falcata	27	99.0	0.0	0.0	0.0	0.0
Ambrosia artemisiifolia	26	33.0	36.7	42.8	18.3	6.5
**Conyza canadensis*	26	58.7	0.0	18.3	0.0	7.5
Carex blanda	20	62.3	18.3	12.2	0.0	0.0
Dichanthelium acuminatum	20	66.0	0.0	6.1	9.2	0.0
**Eragrostis spectabilis*	16	29.3	0.0	0.0	18.3	6.5
Sisyrinchium campestre	15	3.7	0.0	0.0	27.5	11.9
Andropogon scoparius	14	0.0	0.0	0.0	0.0	15.1
Poa pratensis	11	0.0	0.0	61.1	9.2	0.0
Dalea enneandra	10	0.0	0.0	0.0	0.0	10.8
**Solanum ptycanthum*	10	0.0	0.0	6.1	9.2	8.6
Andropogon gerardii	9	0.0	0.0	18.3	27.5	3.2
Dichanthelium wilcoxianum	9	0.0	0.0	12.2	0.0	7.5
**Potentilla norvegica*	9	3.7	0.0	36.7	0.0	2.2
**Typha* species	7	11.0	0.0	6.1	0.0	3.2
Aster ericoides	6	0.0	0.0	18.3	0.0	3.2
Ambrosia psilostachya	5	0.0	0.0	18.3	0.0	2.2
Medicago lupulina	5	0.0	0.0	0.0	27.5	2.2
Nepeta cataria	5	0.0	91.7	0.0	0.0	0.0
Asclepias verticillata	4	0.0	0.0	0.0	0.0	4.3
Bouteloua curtipendula	4	0.0	0.0	0.0	0.0	4.3
**Euphorbia maculata*	4	0.0	0.0	24.4	0.0	0.0
Juniperus virginiana	4	11.0	0.0	0.0	0.0	1.1
**Oenothera biennis*	4	3.7	18.3	0.0	0.0	2.2
**Panicum capillare*	4	3.7	0.0	0.0	9.2	2.2
Morus alba	3	7.3	0.0	0.0	0.0	1.1
**Verbena bracteata*	3	3.7	0.0	0.0	0.0	2.2
Viola pratincola	3	7.3	0.0	6.1	0.0	0.0
**Zea mays*	3	11.0	0.0	0.0	0.0	0.0
Anemone cylindrica	2	0.0	0.0	0.0	0.0	2.2
Asclepias syriaca	2	7.3	0.0	0.0	0.0	0.0
Bromus inermis	2	0.0	0.0	12.2	0.0	0.0
**Eupatorium rugosum*	2	0.0	0.0	0.0	0.0	2.2

Table 2, continued

Hedeoma hispidum	2	0.0	0.0	0.0	0.0	2.2
Astragalus lotiflorus	1	0.0	0.0	0.0	0.0	1.1
Cirsium species	1	0.0	0.0	0.0	0.0	1.1
Echinacea angustifolia	1	0.0	0.0	0.0	0.0	1.1
Euphorbia dentata	1	3.7	0.0	0.0	0.0	0.0
Lactuca species	1	3.7	0.0	0.0	0.0	0.0
**Lepidium densiflorum*	1	3.7	0.0	0.0	0.0	0.0
**Lepidium virginicum*	1	0.0	0.0	0.0	0.0	1.1
Muhlenbergia cuspidata	1	0.0	0.0	0.0	0.0	1.1
**Parietaria pensylvanica*	1	3.7	0.0	0.0	0.0	0.0
Polygala verticillata	1	0.0	0.0	0.0	0.0	1.1
Rhus glabra	1	3.7	0.0	0.0	0.0	0.0
Rubus species	1	3.7	0.0	0.0	0.0	0.0
**Setaria viridis*	1	3.7	0.0	0.0	0.0	0.0
Sorghastrum nutans	1	3.7	0.0	0.0	0.0	0.0
Sporobolus asper	1	3.7	0.0	0.0	0.0	0.0
**Veronica peregrina*	1	0.0	0.0	0.0	0.0	1.1
Viola pedatifida	1	0.0	0.0	0.0	0.0	1.1
Total	1100	1176.9	769.9	1209.9	751.6	492.8

decline in seed populations along an environmental gradient is due to increasing environmental stress. Environmental stress in the Loess Hills, in the form of increasing soil temperature and decreasing soil moisture, generally increases with increasing elevation in the landscape. Increasing environmental stress, leading directly to reduced seed production and seed persistence, is one explanation for the decline in total seed density observed along the transects from deciduous woodland to mid-grassland. This assumes uniform potential seed production among many different plant species, thus a second explanation invokes an indirect effect of environmental stress manifest in the species turnover that occurs along the gradient from woodland to mid-grass. The species that comprise the mid-grass community may have a lower inherent seed productivity. A third explanation is that seeds are being carried by gravity or erosion to positions lower in the landscape. However, since very few seeds of native grassland species were found in the woodland communities, this explanation does not seem as likely.

The high total seed density observed in the exotic grasslands at both sites presents a non-conformity in the seed density/environmental stress gradient. Certainly one factor that must be considered as an explanation is higher seed production by certain species in the community. Since we did not measure fecundity, conclusive statements are not possible. However, if the relatively high seed densities of Kentucky bluegrass (*Poa pratensis* L.), yellow wood sorrel, Norwegian cinquefoil (*Potentilla norvegica* L.), and spurge (*Euphorbia glyptosperma* Engelm.) in the seed bank of the exotic grasslands (Tables 1 and 2, densities compared among communities) are a result of on-site seed production, disturbance may also be an important factor affecting seed densities. High seed densities may be a common feature of disturbed communities since the disturbances generally favor species capable of high seed production.

Table 3 presents a community by community comparison of the composition of the seed bank with that of the vegetation at site 1 and the Pearson correlation coefficients obtained from each comparison. (This comparison was only made for the communities at site 1). The main feature displayed by all five communities is dissimilarity between the seed bank and vegetation (a positive correlation coefficient significantly different from 0 would indicate a similarity). Generally, species that have high relative abundance in the seed bank exhibit low relative abundance in the vegetation, and conversely those species that dominate the vegetation typically make up a minor proportion of the seed bank. This lack of correlation has been reported widely in the seed bank literature, e.g., in Colorado subalpine forest (Whipple 1978), natural grasslands and pastures in Wales (Chippindale and Milton 1932), tallgrass prairie in Illinois (Johnson and Anderson 1986), in Kansas (Abrams 1988), and in Missouri (Rabinowitz 1981), prairie pothole wetlands (Wienhold and van der Valk 1989), and in a California bunchgrass community (Major and Pyott 1966).

The ecological significance of this pattern seems to be that the perennial species that characterize these plant communities do not rely on the production of persistent seed as a

Table 3. Comparison of the relative composition of the seed bank (% relative density) and vegetation (% relative index score) among communities at site 1. Species with relative occurrence greater than or equal to 2% in either seed bank or vegetation are given. Pearson correlation coefficients and the probability the coefficient = 0 are given for each community.

Deciduous Woodland Community (DW) r = -0.448, p = 0.054

SPECIES	SEED BANK	VEGETATION	
Eupatorium rugosum	14.0	1.7	
Verbena stricta	12.0	0.0	
Nepeta cataria	8.7	0.1	
Sporobolus cryptandrus	7.6	0.0	
Parietaria pensylvanica	7.4	0.0	
Conyza canadensis	6.3	0.0	
Rubus species	5.1	4.0	
Solanum ptycanthum	4.7	0.0	
Poa pratensis	3.4	7.3	
Teucrium canadense	3.2	3.9	
Fragaria virginiana	[1]2.3	4.1	
Typha species	2.3	0.0	
Carex blanda	2.1	2.3	
Muhlenbergia racemosa	2.1	0.3	
Cornus drummondii	0.4	32.9	(82% tree)
Viola sororia	1.3	10.6	
Symphoriocarpus species	0.0	8.8	
Ulmus species	0.0	6.5	(94% tree)
Fraxinus pensylvanica	0.0	3.3	(80% tree)

Deciduous Shrub Community (DS) r = 0.007, p = 0.979

SPECIES	SEED BANK	VEGETATION	
Poa pratensis	26.9	13.6	
Verbena stricta	15.4	0.0	
Muhlenbergia racemosa	7.7	0.2	
Sporobolus neglectus	4.8	0.0	
Sporobolus cryptandrus	4.3	0.0	
Conyza canadensis	3.9	0.0	
Anemone cylindrica	3.4	1.5	
Geum canadense	3.4	0.0	
Fragaria virginiana	[1]2.9	4.8	
Sorghastrum nutans	2.9	1.4	
Parietaria pensylvanica	2.4	0.0	
Cornus drummondii	0.5	42.3	(54% shrub)
Symphoriocarpus species	0.0	7.7	
Teucrium canadense	1.0	7.2	
Amorpha canescens	0.0	4.1	
Andropogon gerardii	0.0	2.9	
Ceanothus herbaceous	0.0	2.2	

Table 3, continued

Exotic Grassland Community (EX) r = 0.474, p = 0.055

SPECIES	SEED BANK	VEGETATION	
Poa pratensis	32.7	19.6	
Verbena stricta	20.8	0.0	
Heuchera richardsonii	8.2	5.7	
Sporobolus asper	6.3	0.6	
Amorpha canescens	4.4	6.8	
Ceanothus herbaceous	4.4	11.3	
Sorghastrum nutans	3.8	4.4	
Muhlenbergia racemosa	3.1	0.0	
Anemone cylindrica	2.5	4.2	
Bouteloua curtipendula	2.5	1.3	
Helianthus rigida	0.0	8.8	
Andropogon gerardii	0.0	7.2	
Rosa species	0.0	5.8	
Cornus drummondii	0.0	5.8	(100% shrub)
Fragaria virginiana	0.0	4.1	
Symphoriocarpus species	0.0	4.0	
Aster ericoides	1.3	3.5	

Tallgrass Community (TG) r = -0.239, p = 0.357

SPECIES	SEED BANK	VEGETATION	
Verbena stricta	51.3	0.0	
Sporobolus asper	8.2	0.2	
Conyza canadensis	4.8	0.0	
Ceanothus herbaceous	4.5	5.7	
Sporobolus neglectus	3.4	0.0	
Amorpha canescens	3.0	9.0	
Dichanthelium oligosanthes	3.0	1.0	
Poa pratensis	3.0	3.4	
Andropogon gerardii	0.4	33.0	
Cornus drummondii	0.0	8.7	(100% shrub)
Helianthus rigida	0.0	5.4	
Andropogon scoparius	0.0	4.6	
Fragaria virginiana	[1]1.9	4.1	
Symphoriocarpus species	0.0	4.1	
Bouteloua curtipendula	1.1	3.8	
Aster ericoides	0.4	3.6	
Rosa species	0.0	3.2	

Table 3, continued

Mid-grass Community (MG) r = -0.331, p = 0.293

SPECIES	SEED BANK	VEGETATION
Sporobolus asper	38.0	2.0
Verbena stricta	19.0	0.0
Amorpha canescens	17.4	9.3
Conyza canadensis	4.1	0.0
Bouteloua curtipendula	3.7	18.8
Solidago rigida	2.9	3.2
Andropogon scoparius	0.4	19.0
Andropogon gerardii	0.0	16.9
Gaura coccinea	0.4	6.6
Commandra umbellata	0.0	6.5
Solidago missouriensis	0.0	3.2
Muhlenbergia cuspidata	0.8	2.3

[1] Relative seed bank density of *Fragaria virginiana* contains an unknown amount of *Potentilla norvegica*.

mechanism of maintenance in the community. In general, perennial species allocate a higher proportion of their resources to vegetative growth and less to seed production (Grime 1979). Annual and biennial species generally allocate high proportions of their resources to the production of long-lived seed. This dichotomy in life history strategies seems to be a logical reason for dissimilarity between the composition of the seed bank (represented by the long-lived seeds of short-lived annuals and biennials that have a history on the site) and the vegetation (represented by long-lived perennials with relatively short-lived seeds). However, in our study the species exhibiting the greatest abundance in the seed banks were primarily perennial species that characteristically inhabit disturbed sites. The flora of central North American grasslands is fairly depauperate in annuals and biennials, and ruderal perennials appear to function as ecological replacements.

What then can be said about communities that display similarity between seed bank and vegetation? Fenner (1985) has suggested that such similarity usually exists in frequently disturbed habitats. In this study the exotic grassland community may represent such a situation. Although there was no overt evidence of disturbance in the exotic grassland at site 1, it was located at the interface between woodland and grassland (Figure 3), and there may be a possibility that a "covert, internally-generated" disturbance factor (e.g., perhaps invading gray dogwood) is present.

Potential for Restoration from the Seed Bank

We found 29 native species of extant Loess Hills grassland (based in part on Novacek et al. 1985 and on personal observation) in the seed banks of the woody and exotic grass communities at sites 1 and 7. However, a satisfactory measure of the potential of the seed bank for restoration must also consider the value of seed bank species in terms of their importance and likelihood of natural immigration. A Value Index, that can potentially range from 0 to 99, was calculated for each of the 29 species (Table 4). The index combines a species's abundance rank in extant grassland in the Loess Hills (based on 240 community samples throughout the Loess Hills, unpublished data of the authors) with a measure of its quality (based on its fidelity to prairie and response to disturbance, Pearson and Leoschke 1989).

The deciduous and coniferous woodland communities, which likely represent habitats the most distant temporally from native grassland, had seed banks with very few "good" grassland species. (The term temporal distance refers to the elapsed time between two communities at the same site. It follows from the fact that variation or change occurs at both spatial and temporal scales). The deciduous and coniferous woodland seed banks at sites 1 and 7 contained a total of six species with a Value Index above 44 (for a cut-off we arbitrarily selected the top one-third). Small amounts of blue-eyed grass (*Sisyrinchium campestre* Bickn.), thimbleweed (*Anemone cylindrica* A. Gray), Scribner's panic grass (*Dichanthelium oligosanthes* (Schult.) Gould), Indian grass (*Sorghastrum nutans* (L.) Nash), western ragweed (*Ambrosia psilostachya*) and tall dropseed (*Sporobolus asper* (Michx.) Kunth) were present. The last two species were probably overrated by Pearson and Leoschke (1989) and in our view do not represent high value species. Thus there are only small amounts of four "good" grassland species in the woodland seed banks.

The seed bank of the deciduous shrubland at site 1 contained at least seven species with a Value Index above 44. In addition to the first five species listed above for the woodland seed banks, side-oats grama (*Bouteloua curtipendula* (Michx.) Torr.) and prairie violet (*Viola pedatifida* G. Don) were also observed. Unlike the woodland seed banks, the shrubland seed bank contained some grassland species in moderate density (e.g., Indian grass at 37 seeds/m^2, thimbleweed at 43 seeds/m^2).

The seed banks of the exotic grassland communities at sites 1 and 7 had a total of ten grassland species with a Value Index above 44, including lead plant (*Amorpha canescens* Pursh), heath aster (*Aster ericoides* L.) and big bluestem (*Andropogon gerardii* Vitman). Of the four post-settlement communities, seed densities of high value grassland species were greatest in the exotic grassland seed bank.

The pattern of increasing diversity and density of grassland species in the seed bank from the woodland community to the shrubland and finally the exotic grassland can be explained by the spatial and temporal gradients encompassing these communities. On the north aspect at site 1 (Figure 3), the exotic grassland, shrubland, and woodland are increasingly distant in space from extant native grassland. Likewise, exotic grassland, shrubland, and woodland likely have increasing temporal distance from the presettlement native grassland that formerly occupied these habitats. In fact, the exotic grassland and shrubland communities at site 1 are spatially and/or temporally close enough to extant native grassland that they still contain many native grassland species in the vegetation (Table 3). Many of the grassland species that were observed in the seed bank of these two communities were also observed in the vegetation of the communities. Therefore our measurement of the seed bank as a source of persistent seeds for restoration is confounded by the possibility that the seeds observed were recently produced by plants in the vegetation.

Restoration of a habitat that contains both seeds and plants of desired species is more likely to succeed than that of a habitat that contains only seeds. The presence of remnant plants is a considerable advantage in any natural restoration project. It may be (although this has not been shown conclusively in the literature) that in situations where remnant plants and viable seeds of desired species are both present, the presence of the seeds is inconsequential to the results. Therefore, a habitat without remnant plants provides the ultimate test of the potential of the seed bank, and in this study examples of such habitat are the woodland communities. Very few desired grassland species occur in the woodland seed banks; thus, it appears that the seed bank cannot be expected to contribute significantly to the restoration of native grasslands in the Loess Hills.

While we did determine that minimal amounts of grassland seed were present in the woodland seed banks, we did not determine how those seeds arrived there. On the surface this may seem unimportant compared to the fact that there is seed present. But, with respect to a better understanding of plant biology and ecology, and arguably also from the point of restoration, the origin of the seed we observed in the woodland seed bank is important. Two possibilities exist for their presence: transport across space (i.e., seed dispersal is the mechanism responsible) or transport through time (i.e., persistent seed viability is the mechanism responsible). If the transport mechanism was across space, then there still may be a chance for a moderately successful restoration, especially if there are nearby sources of desired seed. In the Loess Hills, this is often the case because of the adjacent, native grassland communities. If the transport mechanism was through time, then the restoration is likely dependent on a diminishing resource (i.e., a dying seed bank), which must lower the probability that restoration will succeed.

The general scarcity of seeds from perennial grassland species in the seed bank of adjacent communities that are either spatially or temporally close to extant grassland suggests two conclusions. The first is that seed dispersal by these perennial species is fairly limited, and the second is that seed longevity of these perennial species is relatively short. Platt and Weis (1977) measured dispersal distances of seven species that colonize badger disturbance areas in prairie by releasing propagules into the wind (10-15 km/hr) from their natural height. Average dispersal distances of three genera (*Mirabilis, Verbena, Oenothera*) ranged from 0.4 m to 1.8 m, *Solidago rigida* L. averaged 4.9 m, and three genera (*Asclepias, Apocynum, Cirsium*) ranged from 13.8 m to 25.7 m. Their results suggest that some wind dispersed species can achieve adequate distance for movement from extant grassland to adjacent woodland.

Rabinowitz and Rapp (1981) investigated the dispersal capabilities of seven prairie grasses and made relative comparisons between common and sparse species. In general, they showed that in the laboratory and when released from the same height, sparse species had greater dispersal capability than common species. They also made seed dispersal measurements in the field with sticky traps placed at intervals from 0 m to 2 m away from isolated clumps. Their linear regressions indicate that for little bluestem (*Andropogon scoparius* Michx.), big bluestem, and Indian grass, the percentage of the total seed recovered that occurred in the 2 m traps was approximately 2.3%, 0.8%, and 8.9%, respectively. These results suggest that these common, co-dominant prairie

Table 4. Native plant species of extant Loess Hills grassland that were observed in the seed banks of post-settlement communities. Presence is indicated by: L= seed density less than 25 seeds/m^2; M= seed density 25 to 100 seeds/m^2; H= seed density greater than 100 seeds/m^2. See the text for the definition of a species' Value Index.

	Value Index	Woodland	Shrubland	Exotic Grassland
Bouteloua curtipendula	65.4	-	L	M
Viola pedatifida	65.1	-	L	L
Aster ericoides	63.6	-	-	L
Amorpha canescens	63.0	-	-	M
Sisyrinchium campestre	59.5	L	L	-
Anemone cylindrica	58.9	L	M	M
Dichanthelium oligosanthes	54.1	L/M	L	M/H
Andropogon gerardii	54.0	-	-	L
Ambrosia psilostachya	51.5	L	L	L
Sorghastrum nutans	48.1	L	M	M
Sporobolus asper	44.6	L	-	M
Muhlenbergia racemosa	36.5	M	M	M
Sporobolus cryptandrus	35.2	M/H	M	L
Erigeron strigosus	25.8	M	L	L
Heuchera richardsonii	25.0	-	L	H
Rhus glabra	23.2	L	-	M
Ceanothus herbaceous	22.6	-	-	M
Fragaria virginiana	22.0	L	L	-
Dichanthelium acuminatum	17.9	L/M	L	L
Polygala verticillata	17.3	L	L	-
Hedeoma hispidum	14.9	L	-	-
Verbena stricta	13.1	H	H	H
Eragrostis spectabilis	8.0	M	-	-
Aster laevis	7.5	-	L	-
Dichanthelium wilcoxianum	0	-	-	L
Euphorbia glyptosperma	0	L/M	L	M
Oenothera biennis	0	L	L	M
Euphorbia dentata	0	L	-	-
Sporobolus neglectus	0	L/H	M	L

grasses disperse the majority of their seeds close to the parent plant. They did show that Indian grass has a considerably wider dispersal ability than big bluestem and little bluestem.

Information on the dormancy of prairie species is less available. Coukos (1944) investigated the short term dormancy of native grasses under different storage environments. He reported germination rates after 38 months in storage for little bluestem (12%-58%), big bluestem (6%-74%), Indian grass (4%-54%), and side-oats grama (0%-64%). Although the period of storage was not adequate to assess the potential for long term viability, his results suggest these species probably do not persist long enough in the seed bank to contribute viable seeds for restoration. Research on seed dispersal and longevity of grassland species is clearly needed.

Our observations that seed banks in the Loess Hills offer very limited potential for restoration of native grasslands are consistent with similar studies conducted on pasture grasslands and in wetland habitats. Native prairie grasses were successfully restored without seeding in experimental plots on southern Iowa pastures only when remnant plants were present (Rosburg and Glenn-Lewin 1992), because prairie grasses were absent from the seed banks of the pastures (Akey 1989). In seed banks of prairie potholes drained between 5 and 70 years ago, wetlands drained for over 20 years had lost over 60% of their wetland species and 85% of their seed density, suggesting that significant recruitment of wetland species for restoration from the seed bank is limited to wetlands drained for 20 years or less (Wienhold and van der Valk 1989).

SUMMARY

There was a high level of qualitative similarity in the seed bank compositions of the two sites studied. Most likely this similarity arises from the general homogeneity in physical environment and site history between the sites, which is manifest in a general homogeneity in past and present vegetation. Decreasing total seed density along a community gradient from woodland to mid-grassland was apparent and is probably related to a gradient of increasing environmental stress. The more xeric nature of the environment associated with the mid-grassland could cause both lower on-site seed production and reduced seed persistence.

A high level of dissimilarity was observed between the seed bank and the vegetation in the five communities at site 1. The exotic grassland appeared to be the most "disturbed" community, because it had exceptionally high total seed densities and the highest similarity between the seed bank and the vegetation.

The potential contribution of persistent seed in soil seed banks for the restoration of native grassland is very limited. Seed banks of woodland communities, which in our study represented the habitats most distant spatially and temporally from extant native grassland, had very low densities of only three or four native grassland species with high value. Shrubland and exotic grassland communities represented habitats with less spatial and/or temporal distance from extant grassland, and had low to moderate densities of seven to ten grassland species. While the seed banks of exotic grassland and shrubland appear to contain more potential (i.e., more species with higher densities) for grassland restoration, the existence of many of these species in the vegetation (as remnant plants) of the shrubland and exotic grassland communities lessens considerably the importance of these species' presence in the seed bank.

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NATIVE GRASS AND WILDFLOWER SEED: AN LCMR GRANT

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Abstract. In 1991, the Legislative Commission on Minnesota Resources (LCMR) funded research to better manage and utilize a Minnesota natural resource: native plants. In a cooperative effort, the Minnesota Department of Agriculture (MDA) and the University of Minnesota's Department of Horticultural Science undertook a two year project to increase commercial production and improve quality of Minnesota native grass and wildflower seed. The grant supported market research by the MDA to assess supply and demand. The MDA also began to establish seed testing standards and regulations, bringing the native seed industry up to par with other seed industries. The University of Minnesota's Department of Horticultural Science studied the maintenance of genetic integrity in managed systems of native plants. In addition, production techniques and seed yield were evaluated and documented.

INTRODUCTION

A significant portion of the original vegetation of Minnesota was once tallgrass prairie. Tallgrass prairie in Minnesota extended in a roughly diagonal band from the northwest corner of the state to the southeast. Patches of prairie extended east to the Mississippi River (Marschner 1978). Now less than one percent of that original prairie remains in fragmented pieces (Coffin and Pfannmuller 1988). Rich soils which once supported prairie are now being farmed or have been developed as highways, or for urban and industrial use.

Interest in preserving native prairie and restoring degraded prairie habitat has sharply increased over the last two decades. Because of their value as wildlife habitat, low maintenance requirements, and potential for erosion control, the use of native plants has been encouraged for farm retirement programs such as the Conservation Reserve Program and roadside plantings. The Minnesota Department of Transportation (MnDOT) has emphasized the use of native plants as a management tool and a tourist attraction along highways (Bolin et al. 1990). For the same reasons, native species are widely used to restore habitat in Department of Natural Resources (DNR) wildlife refuges and scientific and natural areas. The low maintenance image and aesthetic appeal of native plants have made them attractive to homeowners and for commercial landscaping. Establishment of native plants creates a market for locally derived resources and provides a means of expressing Minnesota's unique regional character. With increased understanding of and appreciation for their assets and the subsequent increased use of native plants, demand has surpassed supply of seed for some Minnesota-origin grasses and wildflowers.

The Legislative Commission on Minnesota's Resources (LCMR) funded the Native Grass and Wildflower Seed research project. The LCMR grant supported basic research leading to better management and utilization of native plants, an increasingly popular Minnesota natural resource. The goal of the research was to enable the industry to meet future demand and to create a more affordable supply of Minnesota-origin prairie plant seed. The results of the research project will hopefully encourage expansion of the commercial production of Minnesota-origin native grass and wildflower seed through the provision of technical information, development of regulatory standards, and analysis of market trends.

DISCUSSION

The LCMR research project is unique because of the multiagency cooperation it has generated. The grant was guided by a steering committee which met quarterly to discuss progress and provide technical guidance. Scientists, policymakers, market specialists, conservationists, and native plant producers were brought together in a process which encouraged interaction and understanding of different viewpoints.

The Minnesota Department of Agriculture (MDA) had administrative responsibility for the grant under the coordination of Charles Dale, Agronomy Services Division. Within the Department of Agriculture, the State Seed Testing Laboratory and the Marketing Division played active roles in carrying out research objectives. At the University of Minnesota, the Center for Alternative Plant and Animal Products (CAPAP) was the nexus of the project. CAPAP was created to aid in the development of new and alternative crops and facilitated completion of work for the grant by contracting with researchers. CAPAP has assisted in realizing new objectives, such as seeking additional funding for the publication of resource materials developed from the research. The Department of Horticultural Science of the University of Minnesota (UM-H) was a major research contributor in the areas of genetics and production. The research cooperators each had a specific area of responsibility which they carried out on their own initiative.

In addition to the active researchers in the MDA and the UM-H, the steering committee was composed of representatives from agencies such as CAPAP, MnDOT, and the DNR. Jack Johnson represented the Agricultural Utilization Research Institute (AURI) which operates within Minnesota to support and facilitate the implementation of new technology into the mainstream agricultural community. The organization of a native plant producers association was facilitated by Jack Johnson of AURI and Dr. Anne Hanchek of the UM-H. To date, the Minnesota Native Wildflower/Grass Producers Association, which formed in 1991, has 9 members. This organization was also represented on the steering committee. Regional interests of the National Wildflower Research Center were represented on the steering committee by Bonnie Harper-Lore.

The research project's five major objectives for 1991 and 1992 were as follows:

1. Development of market information to enable potential investors, producers, and consumers to make sound decisions.
2. Development and standardization of seed purity and seed viability testing methods.
3. Establishment of certification standards to aid in the maintenance of genetic diversity when native species are raised for seed in field plots.
4. Determination of genetic diversity within and between natural populations through morphological characteristics and isozyme analysis.
5. Evaluation and summarization of commercial production practices to provide guidelines to new and existing producers of native wildflowers and grasses.

The MDA Seed Testing Laboratory, under the direction of Michael Muggli, started to develop seed testing procedures for purity and viability for seven species of wildflowers and grasses. For most native species, a standard test has not been established to date. Once established, these standards will enable the producer to have seed tested and labeled in the same manner as that required for traditional crops. This will lead to improved labeling of marketed seed. Tests have been completed on Junegrass (*Koeleria pyramidata* (Lam.) P. Beauv.), prairie cordgrass (*Spartina pectinata* Link.), and purple prairie clover (*Dalea purpurea* Vent.) (taxonomy follows Gleason and Cronquist 1991). These tests must be replicated by additional laboratories before approval of a standard test method and acceptance for publication in the Association of Official Seed Analysts rules. Initial screening was begun on hoary vervain (*Verbena stricta* Vent.), thick spike blazing star (*Liatris pycnostachya* Michx.), prairie dropseed (*Sporobolus heterlepis* A. Gray.), and golden alexander (*Zizea aurea* (L.) Koch.).

Sue Ye, Agricultural Marketing Specialist for the MDA, spearheaded the market analysis research. Ye developed detailed producer and consumer surveys to enable the collection of primary data on the native wildflower and grass seed industry. The surveys were designed to determine current production and consumption levels, as well as to point out trends for future supply and demand for wildflower and grass seed. Information concerning the geographic distribution of seed source and seed destination was requested.

The survey identified current producers and consumers, and potential consumers. It was distributed to nearly thirty producers within Minnesota. Six hundred current and potential consumers were identified and received surveys. Consumer surveys were targeted at nursery and landscape firms, city and state agencies, and special interest groups that might use native species. A database has been developed and will be maintained to manage industry data. This information will be summarized in the final report which will be available by writing the project manager (Dale 1993).

Dr. Harley Otto of the Minnesota Crop Improvement Association has been instrumental in the development of cultural and isolation standards which will ensure that native grass and wildflower germplasm does not significantly change under cultivation for seed production. Certification standards have been written for seed production from native plants.

A primary concern in the cultivation and sale of native plants and seed is the maintenance of genetic diversity. Dr. Mark Strefeler and Kerstin Concibido of the UM-H have conducted research using six model species to evaluate genetic diversity within populations and between regions within Minnesota. Big bluestem (*Andropogon gerardii* Vitman.), little bluestem (*Schizachyrium scoparium* (Michx.) Nash), wild bergamot (*Monarda fistulosa* L.), thick spike blazing star, northern plains blazing star (*Liatris ligulistylis* (A. Nels.) K. Schum.), lacerate blazing star (*L. aspera* Michx.), few headed blazing star (*L. cylindracea* Michx.), and dotted blazing star (*L. punctata* Hook.) were used as the model species. For each of the eight species, several populations were established under cultivation to document morphological differences. Starch-gel electrophoresis was utilized to detect genetic variability based upon separation of enzymes into distinct banding patterns. This information can help to develop guidelines for sound management practices to preserve the genetic diversity of natural and cultivated populations of native plants, and has provided the background information for Otto's cultural and isolation standards.

Dr. Anne Hanchek and Julia Bohnen, also from the UM-H, carried on research involving the evaluation and development of production guidelines. A survey, developed to elicit information regarding facilities, production methods, products being marketed, and the nature of the market was sent to the members of the Minnesota Native Wildflower/Grass Producers Association. A request for a list of problems encountered in harvest and production was included on the survey.

The survey, a literature review, and preliminary research guided the selection of species for further study. Seed was collected from remnant prairies in cooperation with The Nature Conservancy and the Department of Natural Resources. Members of the Minnesota Native Wildflower/Grass Producers Association also cooperated by providing seed. The research of Hanchek and Bohnen addressed two questions developed from responses to the producer survey: how can the rate and uniformity of germination be increased? can seed yield for a species be increased in a cultivated setting versus a native stand?

Twenty-five species were studied in greenhouse germination trials conducted under controlled conditions simulating those of the producers, and/or through a literature review. Prairie cordgrass, wood lily (*Lilium philadelphicum* L.), and prairie phlox (*Phlox pilosa* L.) have been examined in more detail to characterize uniformity and rate of germination in response to stratification and gibberellic acid treatments. Variation in germination response between populations of a species was evaluated. In response to producers' concerns about low seed yield and viability when seed is collected from prairie remnants, field trials were established in May 1992 at the Minnesota Landscape Arboretum to compare seed yield for spiderwort (*Tradescantia* cf. *ohiensis* Raf.), purple prairie clover, and prairie cordgrass in an intensively managed setting versus in the prairie.

CONCLUSION

The LCMR Native Grass and Wildflower Seed project was unique in establishing open lines of communication and cooperation in the development of a new body of knowledge. Industry operators, researchers, and regulatory agencies shared a common goal of making high quality native plant materials more accessible to consumers for many applications. Different perspectives on issues like maintenance of the genetic integrity of Minnesota native plants were aired and, hopefully, will be resolved on the basis of future biological research. New partnerships have been formed and new questions, both basic and applied, have been framed. This exchange of knowledge between organizations and the increased availability of market, seed testing, and production information encourages strong growth of the local-origin native seed industry. Funding for further work has been investigated.

A complete species list, certification standards, germination and yield trial data are available in the final report. An extensive bibliography of prairie plant production literature has also been compiled. Producer guidelines and pictorial seed and seedling identification resources to aid producers unfamiliar with these new crops are being developed. Decisions as to the form of dissemination of this information have yet to be made. CAPAP is assisting in securing funding for publication of the resource materials. Further information about these resources and the final report can be obtained through Charles Dale, project manager, at the Minnesota Department of Agriculture, 90 West Plato Blvd., St. Paul, MN 55107. The final project report will be available after the close of fiscal year 1993.

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HISTORY AND ECOLOGY: THE SIGNIFICANCE OF JAMES C. MALIN'S SCHOLARSHIP

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Abstract. James C. Malin (1893-1979), a pioneering historian of the North American grassland, enlarged the scope of the discipline by integrating the study of history with ecology. Of the scholars of the trans-Mississippi West, Malin's work is probably the least known though the most complex and rigorous. Malin's perceptions of the interrelationship of the physical environment and human occupation, his inter-disciplinary approach to scholarship, his research methods and his publications influenced a generation of historians, geographers and agronomists. Malin interpreted history from an ecological perspective and constructed a theoretical basis for integrating human history and earth history. This integration is of primary importance to those who plan, design and manage the land. His methodological approach to the study of the grassland closely parallels that of the "Annales School" historian, Marc Bloch. Both Malin and Bloch offer a methodological model appropriate to the purposes of those who investigate or create landscapes. Malin's expressed views on the relationship between geographical space, history and public policy provide us with a useful evaluation of how those who influence policy may use or misuse information. Malin's scholarship should not be ignored by those who study the interrelationship between people and the land or by those who shape our landscapes. In this paper, through an examination of Malin's work, I will discuss the relevance of his legacy.

INTRODUCTION

Three scholars have provided the basic theoretical constructs for our understanding of the American West: Fredrick Jackson Turner, Walter Prescott Webb and James Claude Malin (Swierenga 1984). All natives of particular regions of the west, they each confronted long-standing questions pertaining to the landscape and to the significance of people-land relationships. This paper will describe the importance of James C. Malin's scholarship and the relevance of his scholarship to landscape architects.

James C. Malin (1893-1979) is considered the pioneering historian of the North American grassland. He enlarged the scope of the discipline by integrating the study of history with ecology. Of the scholars of the trans-Mississippi West, Malin's work is probably the least known though it is recognized to be the most complex, rigorous and perceptive. It is the very complexity and intensity of his work which has kept it from a wider audience. Malin's perceptions of the interrelationship of the physical environment and human occupation, his interdisciplinary approach to scholarship, his research methods and publications influenced a generation of historians, geographers and agronomists (Swierenga 1984).

As a professor of history at the University of Kansas from 1921-1963, he devoted his career of nearly sixty years to the study of the grasslands. The everyday life of the citizens of Kansas and the Kansas landscape provided the material found in his eighteen books and more than eighty articles.

DISCUSSION

Turner and Webb acknowledge in their respective research the interdisciplinary nature of historical study (Swierenga 1984). However, it is Malin who actually practiced it. Malin immersed himself in the literature of the natural, physical and social sciences. This preparation led him to define the grassland as a unique environment and to describe the social, political and economic forces that contributed to the tension in which people and nature coexisted. (Malin earned three equal majors in college -- history, biology and psychology-philosophy together with a minor in mathematics).

According to Swierenga, it is Malin's ecological interpretation of the grassland that provided the foundation for the "new rural history" that developed in North America during the 1950's (Swierenga 1981). Malin never limited himself to the study of past politics and elites through written records. Rather he studied people and their activities systematically and comprehensively by going into the field. Often he would conduct his field work with people in other disciplines. Malin sought to understand the lives of people and the landscape as it was actually lived in and experienced.

Marc Bloch, a founding father of the Annales school whose relevance to landscape architecture has been demonstrated by Fredrick Steiner, clearly places people in the landscape. Malin's historical concepts and methodology resemble those of Bloch (Bloch 1966, Debien 1947). Bloch, a contemporary of Malin, conducted pioneering studies in the rural history of France. He, too, roamed the rural landscape and immersed himself in the literature of all disciplines which related to land and people. Bloch's work revolutionized French rural history and inspired many young scholars. Both Bloch and Malin urged that history be studied as a whole and that historians should examine specific topics in relationship to a totality. While Bloch and Malin shared many similarities, Malin had no acquaintance with Bloch or other "Annales" scholars (Swierenga 1984).

But like the French scholars, Malin was also a pioneer in the examination and use of quantitative data available in local communities. Malin was motivated to pursue this type of information for at least two reasons:

1) he believed that the significance of local history helped one to understand change in a broader context, and
2) the lack of a scholarly and accurate history of Kansas motivated him to examine these local sources as a means of developing a documentary history of Kansas (Swierenga 1984).

The mass figures found in national census data, Malin argued, were generally inadequate and were often based upon arbitrary and capricious boundaries and, furthermore, masked local variations and differences. Malin contended that history should be written from the "bottom up" and local data are one way to do just that (Malin 1940). The writing of survey history from the "top down", Malin insisted, "partakes too much of the fitting of generalizations from the study of underlying detail" (Malin 1940). The study of local community history also recognizes the fact that people do not live compartmentalized lives. The units of analysis at the community-scale permit one to view the people-land relationship as a whole.

Malin made extensive use of local records -- land records, probates of wills, church and school records and various state and national census schedules of population and agriculture. It was through Malin's research that five major farming zones of Kansas were defined and that assumptions about increasing farm turnover in Kansas were determined to be incorrect. The pattern that emerged was that Kansas farmers were highly mobile during the frontier period, and after World War I a high degree of stability was achieved (Swierenga 1984). For the first time, what was happening to people and the landscape was made very clear. Interstate migration, farm turnover and geographic mobility were all areas to which Malin's innovative techniques were applied. Some of this work produced findings which ran counter to Turner's "Frontier Hypothesis."

In his studies of the American grassland Malin established a different interpretation of the frontier experience. Malin's central thesis is that the agricultural adaptation of European forest-culture people to the treeless grassland environment was a painfully slow and disorganized folk process that succeeded only because of the ingenuity and resourcefulness of individual settlers. The human mind and skills, not geographical space, are the cardinal factors in human progress. The physical environment is determinative only with fairly wide limits of tolerance. Geographical givens set the outer boundaries within which people have freedom to adapt in optimum ways (Swierenga 1984, Malin 1947). In Edwards County, Kansas, Malin used the census records and minutes of the farmer's club to illustrate the processes employed by farmers and ranchers to adapt to the prairie. The selection of suitable crop varieties, culture and tillage were important items of discussion at the club meetings. The care and feeding of livestock also received considerable attention in the minutes. In part, it is through discussions about the practical problems of making a living as a farmer or rancher that enabled the individuals to adapt their agricultural practices to the prairie landscape. As Malin points out, failure to find at least a partial solution meant destitution (Swierenga 1984).

Malin's dictum that the individual is the ultimate creative force in civilization was at the heart of his writings. He thought geographers and historians placed far too much emphasis on geographical space and not nearly enough on people in time and the capacity of people to discover new properties of the earth (Malin 1947). For Malin there was no end to the frontier, no end of geographic space. He believed the human being's capacity to discover new relationships "knows no limit". In short, land use, not land availability, is the critical factor (Swierenga 1984). The frontier remains an open-ended process of the intelligent use of resources.

A key point of Malin's perspective on the landscape and the grasslands in particular is that: throughout time (both geological and historical) all regions of the earth are adequate for all native vegetation and higher life forms within their limits. Human occupants must fit their culture into the natural givens of the environment. Each area is biologically complete; deficient in nothing and successful human habitation depends on using the available natural resources to the best advantage. For example, the plains country is normal for hard spring and hard winter wheats. Western Kansas has a normal climate for grain sorghums and doesn't have enough rainfall for corn. Likewise, Herefords will thrive on the Plains where buffaloes were most numerous but cannot compete with cattle raised in the Bluegrass Region of Kentucky. (Malin 1947).

A region, according to Malin is: never "super" or "sub" anything that constitutes its native condition and is not deficient in anything that constitutes its natural condition. (Malin 1947).

The natural resources of an area are culturally defined by its inhabitants, not by climate, fire or climax formations. Thus, new skills acquired by people create new natural resources, new opportunities and new landscapes. An example which illustrates this point is found in Malin's study of the Bluestem pasture region of Kansas. Malin documents how eastern settlers struggled to overcome their view of the superiority of domestic grasses over native grasses. Haying practices initially employed by the settlers followed the eastern practice of cutting hay during the bloom period. It was only after years of experience that they determined that Bluestem makes the best hay when cut just after mid-summer before it has seeded (Swierenga 1984). The "landscape" that emerged as the occupants began to understand the ecology of the Bluestem pasture region is now regionally and nationally significant for the meat it supplies. The process is indeterminant. In any discipline or activity, human potential is the crucial variable. Each landscape in every place and time is unique and subject to continuously irreversible change due to the interaction of numerous independent variables -- climate, geology, living organisms, and human activities such as transportation and communication.

Malin's description of the relationship between natural resources and the regions of the country anticipates the work of natural resource and regional economists. For example, Perloff and Wingo (1975) in their seminal article, "Natural Resource Endowment and Regional Economic Growth" focus upon the issue of defining "resource endowment". They conclude that a region's wealth is based upon such determinants as preferences, trade requirements, income levels, technology and social organization. As these variables change so will what constitutes the "resource endowment" and the relative advantage of a region supplying that resource. Perloff and Wingo's conclusion, similar to Malin's, is that people and their activities are the crucial variable in understanding the use of natural resources.

As noted by Swierenga, Malin's outstanding contribution was to meld various disciplines as a way to "organize" and "do" regional history. However, Malin's primary interest was the relationship of ideas to actions and the grassland was the vehicle by which he expressed this. Intellectually, he was interested in the presuppositions people have about the universe. He used the concepts of "finished world" and "open world" to describe the views of others. For Malin, if the world was indeed "finished", people would need to learn to live in harmony with nature and restore equilibrium. If it was an "open" world, people would have to learn to live with endless transformations of the environment. According to Malin, most people (scientists, politicians, social scientists, etc.) assumed a "finished" world concept.

Frederick Jackson Turner's "Frontier Hypothesis" dominated American historiography from the 1890's to the 1930's. In his thesis, Turner suggested that people would have to turn more frequently to government planning to preserve the pioneer democracy which had been safeguarded by the freeland frontier environment (Malin 1944). Malin believed that the Progressives and New Dealers had seized upon this concept of "closed space" and had used this as justification for government planning. In fact, Malin went so far as to state:

> That these individuals had distorted Turner's teachings and had created a false Turner legend. Turner's work was used as a respected source upon which to hang their own ideas. Malin 1944

While other historians felt that Malin's judgments about Turner were motivated by political beliefs, it was Malin's research findings that led him to reject the social and demographic patterns of frontier settlement promoted by Turner. Also, since Malin was firmly committed to the notion that ideas have consequences, he was able to link Turner's work to the public policy decisions made during the 1930's.

Malin's work is not above criticism. His analysis of quantitative data was generally unsophisticated. For example, he misread his own evidence and concluded that farmers on the frontier were older than their eastern counterparts (Swierenga 1984). Malin did not portray the cultural diversity of Kansans and his depiction of agricultural history was selective, despite his commitment to holistic history (Swierenga 1984).

He was a prolific author. However, much of his work was privately printed because he was often denied publication through conventional channels. Malin did not always persist after an initial rejection. His place in history is affected, in part, by this and because he had a tough-minded disposition. He was a serious scholar, burdened by his times and willing to forego friendship for research (Swierenga 1984).

Malin enlarged the scope of his discipline by including the natural sciences in his history of people and land relationships on the Great Plains. He is credited, by others, as one of the few people to integrate history, geography and geology as part of historical analysis. Malin believed his primary contribution to be a synthesis of science, technology and history applied in a significant regional setting. He wrote:

> Few scientists are trained in history and social science, and likewise few historians and social scientists have training in science. Malin 1947

CONCLUSIONS

Three major points summarize the significance of James C. Malin's scholarship to landscape architects. First, Turner, Webb and Malin all contributed to our knowledge of American history. Yet the curriculum in most design schools provides little, if any, opportunity to gain an understanding of how these individuals, among others, shaped our understanding of people-land relationships. For example, the history of the conservation movement in this country is inextricably linked to Turner's "Frontier Thesis". This thesis, later refuted by Malin, played an enormous role in shaping public land use policy in this country. Malin's denunciation of this "closed space" world view offers landscape architects an opportunity to analyze past policies and to perhaps more fully understand alternative views.

Second, the content of most landscape architecture studios and history courses concentrates on elite landscapes (both European and American) which reflect very little of the quality of the daily lives of a majority of past, present and future people. Fredrick Steiner in his article "Human Ecology and the Annales School" states: "Knowing good design principles does not ensure the creation of suitable human habitats" (Steiner 1986). Malin's work provides one model (along with the "Annales School") for examining the ways in which people live in an everchanging landscape. In other words, history written from the "bottom up" would yield a different perspective on people-land relationships. Common people, in this view, would move to "center stage" and be considered along with the articulate elites.

Third, for Malin, ecology is not a separate consideration but an integral part of history. In most history courses there is far too little discussion on the ecology of a given place. Villas, cities, gardens and parks should be considered within the context of the landscape along with the prevailing attitudes regarding spatial manipulation. Malin's work in the grasslands of North America offers a model for how such a history might be written. Briefly, it would include:

a. The re-examination of history with specific references to ecological relationships.
    i. behavior analysis/folk processes
    ii. exploration reports
    iii. ecological traverses
b. The collaboration of several disciplines.
c. The use of local data.
d. The units of analysis would be the region and community.

The profession of landscape architecture is concerned with the preservation and protection of natural resources and understanding the interaction of the political, economic and social systems with access to these resources. Landscape architects have the responsibility of reconciling the needs of people and the environment with minimal disruption. James C. Malin's work offers us a perspective on people-land relationships that should not be ignored.

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CITIZEN ACTION FOR BIODIVERSITY AT WOLF ROAD PRAIRIE

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Abstract. Through the discovery, study, preservation and restoration of Wolf Road Prairie, members of Save the Prairie Society and citizens of Westchester, Illinois have managed to retain an 82-acre native tallgrass prairie within the suburban ecological landscape of Chicago, Illinois. They have voiced the belief that one of the few remaining original prairies in Illinois is valued for preservation as a living history museum for future generations. This urban prairie is located just outside of Chicago in a tangled network of commercial franchises, residential homes, and supermarkets. Today, an individual can go to Wolf Road Prairie to study prairie ecology and identify flora and fauna. An individual can volunteer in prairie restoration and maintenance and participate in the annual prairie heritage festival. Or one can simply take a walk along pre-existing sidewalks and paths to enjoy the open space and appreciate the natural beauty of the landscape. Wolf Road Prairie is an example of how citizens for conservation can take action to strike a balance between natural ecology and human ecology.

INTRODUCTION

Environmental professionals, politicians and citizens have come to recognize that the ecological diversity of the planet Earth needs protection. The purpose of this paper is to describe the work of the Save the Prairie Society in fostering environmental awareness in Westchester, Illinois and in preserving Wolf Road Prairie as historic landscape and as a biologically diverse ecological community.

The Save the Prairie Society endeavors to nurture an environmental ethic in the Chicago, Illinois area by maintaining three clearly-stated organizational goals. These goals are preservation, restoration, and education. Members recognize the need for communities to protect local habitat, endangered species, and historic open space (Spale 1990/1991). Wolf Road prairie is located at the intersection of two busy streets in a matrix of gas stations, shopping malls, corporate complexes, and residential housing. (Figure 1). There are several plant communities identified by indicator species found on the 82 acres. These communities are: oak savanna, wetland/marsh, and mesic prairie.

DESCRIPTION

Developing an inventory of species composition is an ongoing project at the Prairie. According to Jack Shouba, prairie specialist, there are 347 total plant species or about one-seventh of all the plants found in Illinois, or in the Chicago region including parts of Wisconsin, Indiana, and Michigan. There are " -- 282 native species, most of which are characteristic of prairie, savanna, woodland, or wetland. Dozens are ... restricted to undisturbed natural environments. Several are rare, threatened or endangered" (Shouba 1992). Currently, Wolf Road Prairie has a Natural Areas Index rating of 80+. "This index takes into account the number of species and the relative conservatism or weediness of each. In *Plants of the Chicago Region*, by Swink and Wilhelm, a rating of 35 or 40 indicates a 'rather profound environmental importance in terms of a regional natural area perspective', while a rating in the fifties or higher indicates 'paramount importance; such areas are extremely rare'." (Shouba 1992) This rating is very good, given the high level of urban population density surrounding the prairie.

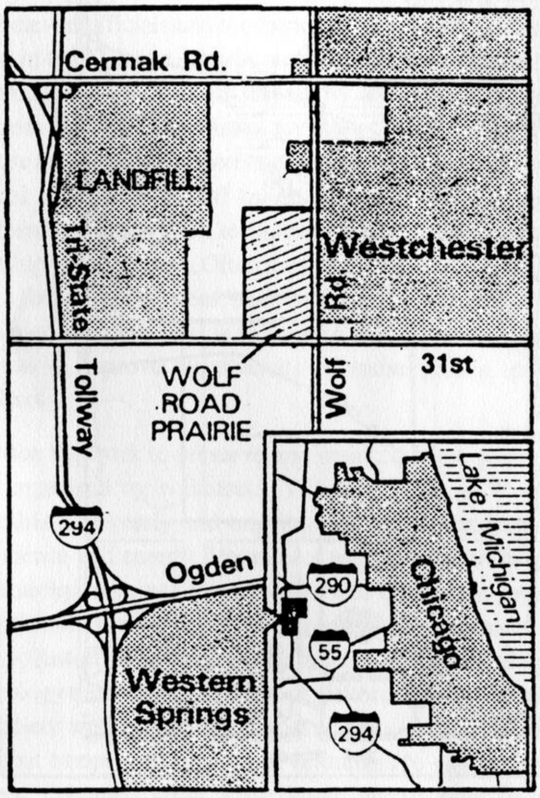

Figure 1. Map of Wolf Road Prairie and its location in the Chicago suburbs.

Observations of volunteers also contribute to a record of visible flora and fauna. For example, on Saturday, May 22,

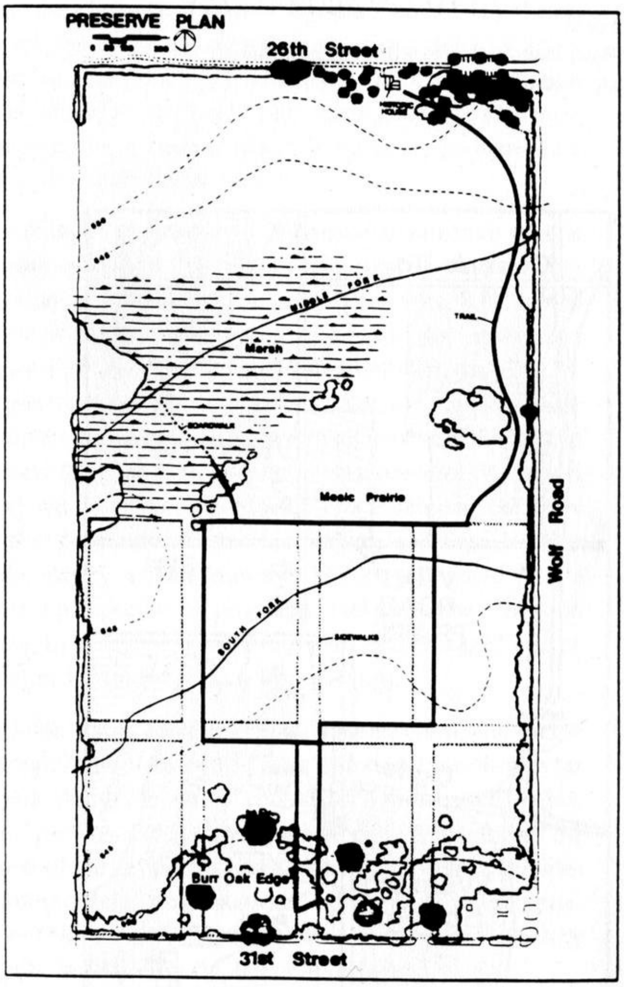

Figure 2. Preservation Plan, showing nature trail, boardwalk, and sidewalks in Harrier Marsh and Wolf Road Prairie.

1993 one male and one female common oriole (*Icterus galbula*) were sighted by restoration volunteers in a tree in the open prairie area. An ancient bur oak (*Quercus macrocarpa*) that is recorded in *Famous and Historic Trees* by Randall and Clepper is found in the savanna area which is close to the woodland area (Save the Prairie Society 1992) (Figure 2). In this area in the spring one finds wild hyacinth (*Carnassia scilloides*), wild geranium (*Geranium maculatum*), and rue anemone (*Anemonella thalictroides*) which is an indicator of undisturbed woodland.

In the wetland area bur reed (*Sparganium americanum*), arrowhead (*Sagittaria latifolia*), water plantain (*Alisma triviale*), swamp milkweed (*Asclepias rubra*), blue flag (*Iris versicolor*) have been identified. Bird life such as mallards (*Anas platyrhynchos*), Canada geese (*Branta canadensis*), and blue-winged teal (*Anas discors*) have been seen in areas of open water. In the prairie area, forbs such as compass plant (*Silphium lacinatum*), rattlesnake master (E*ryngium yuccifolium*), and prairie dock (*Silphium terebinthinacceum*) have been identified, as well as other plants such as blazing star (*Liatris apsera*), wild indigo (*Baptisia tinctoria*) and prairie dropseed grass (*Sporobolus heterolepis*). A combination of woodland, oak savanna, mesic prairie, and wetland/marsh make Wolf Road Prairie a diverse habitat for bird and plant life.

HISTORY

Because Wolf Road Prairie is largely undisturbed, the natural history of the area becomes important in understanding ecological succession. Thousands of years ago glaciers covered northeastern Illinois. As the ice receded, tundra colonized the land and over time changed to pines and spruces. As the climate became warmer and drier, oaks and hickories replaced the coniferous forest. Prairie gradually expanded to the south and west. As recently as 175 years ago, prairie extended over two-thirds of Illinois (Save the Prairie Society 1992). Indians hunted on the Illinois prairies and traded with French explorers from the north and later with English settlers who came from the east. Today, if one stands in the area in Wolf Road Prairie where grasses such as big bluestem (*Andropogon gerardi*) grow, one can experience what it might have been like to be in a prairie at that time. It is as if one is standing in a sea of grasses.

Early pioneers at first regarded the prairie as useless. They could not use wooden plows to cut the grassy roots to cultivate food crops. But with the invention of the steel moldboard plow, farmers converted the land for grazing and cultivation of corn, wheat, and soybean. Today, less than one hundredth of one percent of original grassland remains in Illinois. Wolf Road Prairie is recognized as the largest silt loam priairie east of the Mississippi (Sinopoli 1992). There are several reasons why it was spared the extensive plowing and farming that destroyed so much prairie in Illinois.

Records in Westchester, Illinois state that a small German farm community called Fransozenbusch was founded in 1852 at the intersection of Wolf and Cermak Roads. At that time the area was considered too wet to plow or use for pasture. In the 1920's, the land was parceled into small lots and sold by a developer Samuel Insull (La Force 1986). Village policy at this time emphasized development. However, the Great Depression halted housing construction on the land, creating a unique situation in Wolf Road Prairie's history. World War II diverted landowners' attention away from housing construction and toward the war effort as a few of these lots were used as "victory gardens." (La Force 1986). No water or sewerage lines were constructed. After the Great Depression and World War II, housing construction increased but zoning laws had changed to a larger lot size. The area might have been developed in the 1950's, but confusion over land titles of bankrupt Depression-era landowners caused Wolf Road Prairie to remain a large overgrown vacant lot for thirty more years.

Several prairie specialists were aware of prairie indicator species in the area. Floyd Swink, taxonomist at the Morton Arboretum, knew of the prairie area in the 1940's. From 1974 to 1978, Jack Shouba and several others organized high school students and citizens in local garden clubs to canvass communities for petition signatures and to raise money to buy lots. They organized to convince local government officials that, due to public interest, Wolf Road Prairie should be preserved. In the meantime, a complex and obscure pattern of ownership continued to be largely responsible for preventing resale and rezoning of the land for development (La Force 1986). Today the grid of original plots is used for recording locations of endangered species or rare plants, and conducting ecological studies.

In 1975 high school students, under the direction of Jack Shouba, grew plants to sell at plant sales. Because of several of these efforts, a lot, funded by the Lyons Township High School Conservation Club, was purchased by the Save the Prairie Society in 1975 (La Force 1986). Another lot was purchased by the La Grange Park Garden Club.

Members of Save the Prairie Society began to actively participate in the community and in local government. They published brochures for distribution at libraries, churches and supermarkets, and they printed petitions for volunteers to gather signatures of citizens supporting preservation. They attended Village of Westchester and Park district board meetings to advocate preservation.

In 1978, a chapter of Save the Prairie Society was formed in the town of Westchester to give the citizens of Westchester a stronger voice in land use decisions concerning the prairie. In 1980 the Illinois Natural Areas Inventory determined that Wolf Road Prairie was priority land for preservation. In 1984, State Representatives Judy Baar Topinka and Ted Leverenz co-sponsored a special $250,000 appropriation for land purchases. This followed a $350,000 special appropriation which initiated land purchase by the Illinois Department of Conservation. With this funding, the Prairie received statewide recognition and greater public support. The Save the Prairie Society continued its work with the media by writing editorials and articles in local newspapers, gathering information, organizing prairie walks, and announcing festivals and activities for children. The educational work of Save the Prairie Society convinced State officials of the historic and ecological value of Wolf Road Prairie.

THE PRAIRIE TODAY

Today, Wolf Road Prairie is a nature preserve protected by law, jointly owned by Cook County and the State of Illinois. It has been nominated as a National Natural Landmark and is under the volunteer stewardship of the Save the Prairie Society. The Save the Prairie Society consists of a core group of eleven officials and thousands of volunteers and supporters in the Chicago suburbs and is working to expand its role throughout the State of Illinois by developing the Natural Areas Rescue Fund. Areas for preservation throughout the state are identified as potential preservation projects, with the goal of arranging land trusts and negotiating agreements whereby conservation techniques are used while land ownership is maintained. Often these areas are very small in size, are found in rural areas, and require a small amount of funds to purchase. The goal is to create a chain of small preserved areas to improve the diversity of native prairie species in Illinois.

Often the work to preserve and maintain these prairie areas is organized by volunteers. Volunteer work at Wolf Road Prairie is a yearly and ongoing activity that requires great patience and energy. Volunteers are working on the prairie Saturday mornings from February to December, regardless of the weather. Every third Saturday of the summer months a volunteer is present in the afternoon to conduct prairie ecology tours to small groups of visitors. The Save the Prairie Society works with high school ecology clubs, Boy and Girl Scout troops, and individual volunteers to gather seeds, reseed degraded areas, clear brush encroaching on prairie plants, and burn specified areas (McDermott 1992). Both Boy Scouts and Girl Scouts sponsor merit badges rewarding ecological restoration work at the Prairie. On specified days throughout the year, a visitor can see and work with volunteers working on a targeted area. For example, on Saturday, May 22, 1993, four volunteers pulled garlic mustard (*Alliaria officinalis*) from a section of the wooded area. In 1991, fifty-two volunteers contributed 1,933 hours toward restoration (McDermott 1992). Restoration work is considered as the core task for preserving rare prairie habitat. This is so that visitors may walk in the Prairie to appreciate the value of prairie as open space and natural heritage.

To assist visitors in their appreciation of prairies, Save the Prairie Society members designed and developed a self-guided nature tour with an accompanying brochure. This is a major accomplishment which fosters understanding of the prairie landscape and its history to change perceptions of prairie habitat. Visitors take a brochure from a kiosk located at the beginning of the trail. As they encounter stations along the trail, they learn about the basic characteristics of a prairie. People are invited to observe and experience the natural prairie landscape in its restored beauty; to learn to identify savanna, prairie, and wetlands; to find prairie indicator species; and to observe birds and animals in the area. Colors and seasons are described, as are glacial landscape processes, and the overriding importance of fire in preserving the prairie ecology. Sometimes it takes one observation of a red-tailed hawk soaring over waving prairie grasses to awaken a conservation ethic in an individual.

The Save the Prairie Society has a management plan for Wolf Road Prairie. The mission of the management plan is to increase biological diversity of species in the Chicago area, the United States and globally. The goals of the plan are the following: use land ethics (wise ecological restoration procedures), maintain aesthetically pleasing open space, and encourage the education of citizens of all ages to learn and to appreciate the natural history of their region in order to contribute to the overall health and well-being of the Chicago area.

Preservation and restoration activities range from land acquisition for buffer zones to physical restoration such as cutting of brush and clearing of trees and woody non-prairie plants. When Wolf Road Prairie was known by prairie specialists as an open area, there were clearly recognizable but small areas where indicator species could be located. Today, by clearing invader species and woody plants, girdling trees, removing weeds, burning, and reseeding, open areas of prairie are beginning to change to look more like distinctive prairie landscape.

Prescribed burns are also conducted periodically to control woody shrubs such as two species of buckthorn, common european buckthorn (*Rhamnus cathartica*) and glossy buckthorn (*Rhamnus frangula*), gray dogwood (*Cornus racimosa*), and boxelder (*Acer negundo*). There are more forbs than grasses in some areas. This creates less dry grassy burning material to spread a fire. Therefore, prescribed burns are difficult to conduct over large areas of prairie.

Burns have been conducted in the spring and the fall in different areas to burn weeds and to allow sun to penetrate the earth. This is to clear dead winter underbrush, release minerals to the soil and stimulate growth of deep-rooted prairie plants. For example, in 1990 prescribed burns of 25 acres were conducted in spring and fall of that year (McDermott and Godson 1990/1991). According to local folklore as recounted by a 90-year-old resident, the Village of Westchester volunteer fire department used to set fires in one particular area of the prairie to practice fire fighting (McDermott 1993). Today that particular area is one of the best areas for identifying prairie indicator species.

Major restoration problems at the prairie center on buckthorn, honeysuckle (*Lonicera japonica*), gray dogwood, and boxelder removal after prescribed burns. These green shrubby plants do not burn very well. To prepare fall fire breaks and to remove green shrubby plants that resist fire, a sickle-bar mower is used (Godson 1990/1991). The sickle bar mower is proving effective in preventing further growth of the green shrubby plants. Although results of these restoration activities are difficult to quantify, those who have worked on restoration over the past years notice an increase in variety and numbers of prairie forbs and grasses. Often a species that was thought not to be growing in the prairie will bloom when favorable conditions have been created. Prairie specialists are now developing quantifiable formal studies to study and record these conditions and changes.

The third activity of the Save the Prairie Society is education. People of all ages are invited to participate in the conservation and enjoyment of Wolf Road Prairie. Special tours are designed for children to introduce them to common plants and animals, principles of ecology, as well as Indian lore. A character named Hody Coyote is frequently featured in the "Prairie Pointer," in the self-guided nature trail brochure, and at Prairie Festivals. Hody Coyote gives advice on prairie preservation and tells stories about the Indians and animals that live there.

Bird and plant identification tours, photo seminars, cookouts, and night insect identification walks are organized by the Save the Prairie Society for adults (Godson 1992). Townspeople come to the prairie to observe and enjoy, to draw, paint, and photograph the flowers, plants, trees, and animals found there. These drawings, paintings, and photographs have gradually become a record of the flora and fauna identified through the seasons (Gitts 1990/1991). A broader goal of Save the Prairie Society is to find a balance between contemporary human activities and a natural ecological system that is thousands of years old.

For many years Wolf Road Prairie was thought of as a vacant lot located behind a gas station. The previous perception of prairies as useless land has changed largely because of the efforts of citizens' groups such as Save the Prairie Society. They recognized that a rare natural resource in Illinois is disappearing and are working to preserve as much as possible.

Former U.S. Senator Gaylord Nelson, the founder of Earth Day, stated in a speech to U.S. Environmental Protection Agency employees that the overriding purpose of Earth Day was to bring attention to the most important issue of our day, the health of the resource base of our planet. He further stated that it is time to nurture a conservation generation with an environmental ethic (Nelson 1992). In a time when prairie has been almost completely lost to farming, grazing, and urban sprawl, it is imperative to preserve the last biological remnants. A number of citizens' environmental groups in the Chicago area, wishing to preserve these remnants, have organized a Wilderness Day. In 1993, the Wilderness Day was held on August 8th at the Wolf Road Prairie. As citizens of Westchester and surrounding towns become aware of Wolf Road Prairie and its unique role in the natural heritage of the landscape, they too, express strong concerns for the resource base of the planet and the value of encouraging a conservation ethic.

The work of Save the Prairie Society to preserve and restore Wolf Road Prairie and to educate the public underscores the value of providing a natural heritage indigenous to Illinois now and for future generations. The process of preserving Wolf Road Prairie has been controversial, but the indefatigable efforts of many dedicated persons and organizations, and above all, those of the Save the Prairie Society have created opportunities for individuals to interact with the prairie landscape, to appreciate its history and beauty, and to work toward nurturing a global conservation ethic.

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The statements made in this article reflect the viewpoint of its author and not necessarily those of the U.S. Environmental Protection Agency.

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SWITCHGRASS: A POTENTIAL BIOMASS ENERGY CROP FOR ETHANOL PRODUCTION

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Abstract. One of Canada's leading strategies for CO_2 reduction is the development of a biomass energy industry. Dedicated energy crops need to be used for the large scale, sustainable development of this industry. Switchgrass (*Panicum virgatum*) has been identified as the model herbaceous energy crop species by the United States Department of Energy. It is a warm season (C_4), perennial grass which is native to the southern Canadian prairies and Eastern Canada. Switchgrass has many characteristics which make it suitable for a biomass energy crop including: high productivity; low N, P and K requirements; high moisture use efficiency; stand longevity; soil restoring properties; disease and pest resistance; adaptation to marginal soils; and low cost of production. A cellulosic ethanol industry based on warm season grasses, unlike the grain ethanol industry, offers significant potential for CO_2 reduction. Energy crop production from C_4 perennial grasses will increase carbon storage compared to current land use by increasing above and below ground biomass and soil organic matter levels. CO_2 emissions will be reduced substantially compared to a fossil fuel based industry because switchgrass is a renewable feedstock with a high energy output/input ratio and because lignin (the byproduct of the cellulosic conversion) is used as an internal energy source for the conversion process.

INTRODUCTION

Using a complete material cycle analysis, Pimentel (1991) concluded that ethanol production from grain does not provide energy security, is not a renewable energy source, is uneconomical and increases environmental degradation. While other crops such as trees or perennial grasses are better than annual grains in terms of energy and the environment, the technology to economically convert these materials into ethanol has been inadequate. However, recent advances in cellulosic conversion technology has made it possible to efficiently convert dedicated energy crops such as fast growing trees and warm season grasses into ethanol. With further investment in cellulosic conversion research it is anticipated that a cost competitive process with gasoline could be achieved by the end of the decade (Figure 1). The main processes in conversion of the cellulosic biomass are: 1. steam or chemical pretreatment (which breaks the lignin bonds and makes carbohydrates available for enzymatic conversion); 2. enzymatic hydrolysis (converts the carbohydrates into fermentable sugars); 3. fermentation; 4. distillation; 5. residue processing (the lignin that is leftover after the extraction of ethanol is mechanically dewatered and burned to provide the steam and electricity to drive the entire conversion process).

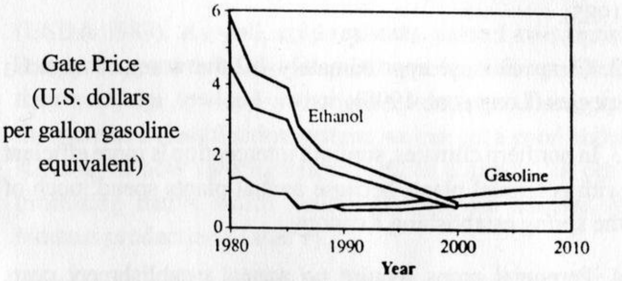


Figure 1. Past and projected costs (1988 basis) for ethanol and gasoline (Lynd et al. 1991). The range of future gasoline prices is based on U.S. Department of Energy oil gasoline price projections. For ethanol, prices are estimated from past research and an aggressive program for future research. The range shown arises from assumed capital recovery, with the higher values being for a capital recovery factor typical of private financing and the lower values being for a capital recovery factor more likely for municipal or utility financed structure.

Developing Low Cost Feedstocks

The recent advances in cellulosic conversion technologies is stimulating interest in low cost farm derived energy feedstocks. Crop production strategies need to be developed which are as efficient as possible in capturing sunlight (solar energy) and storing it in plants (solar battery). Focusing on energy efficiency will lead to low cost energy feedstock production. Desirable characteristics for energy feedstocks include:

1. Efficient conversion of sunlight (solar energy) into plant material (solar battery);

2. Efficient water use as moisture limitation is one of the primary factors limiting biomass production in most of North America;

3. Capture of sunlight for as much of the growing season as possible;

4. Minimal external inputs in the production and harvest cycle (ie. seed, fertilizer, machine operations and crop drying).

We know that to achieve these objectives several issues need to be considered:

1. There are two main photosynthetic pathways for converting solar energy into plant material: the C_3 and C_4 pathways. The C_4 pathway is approximately 40% more efficient than the C_3 pathway in accumulating carbon (Beadle and Long 1985).

2. C_4 species use approximately 1/2 the water of most C_3 species (Long et al. 1990).

3. In northern climates, sunlight interception is more efficient with perennial plants because annual plants spend much of the spring establishing a canopy.

4. Perennial crops require no annual establishment costs (seed, tillage etc.) and are N efficient because N can be internally cycled to the root system in the fall (Clark 1977). Nutrient leaching and surface nutrient loss through soil erosion is minimal with perennial crop production compared to annual crop production. C_4 grasses have a higher N use efficiency than C_3 grasses (Brown 1985).

Based on these criteria, the fastest, most resource efficient crops to grow would be perennial C_4 grasses. Since 1986 the US Department of Energy (DOE) has evaluated herbaceous and woody biomass crops for biomass production. It is not surprising then that the lowest cost feedstock production that has been achieved has been with switchgrass (*Panicum virgatum*), a C_4 prairie grass. Several studies have estimated costs at $30.00/tonne (Sladden et al. 1991, Parrish et al. 1990).

Rationale For Switchgrass As A Bioenergy Feedstock

High Productivity:
When appropriate cultivars are chosen, productivity is high across much of North America. Yields of 20 to 30 t/ha have been obtained with lowland switchgrass ecotypes in Alabama (Sladden et al. 1991). In studies near the Canadian border, winter hardy upland ecotypes of switchgrass have produced yields of 9.2 t/ha in northern North Dakota (Jacobson et al. 1986) and 12.5 t/ha in northern New York (Thomas and Lucey 1987).

Moisture Efficient:
Switchgrass uses water approximately twice as efficiently as traditional cool season grasses (Stout et al. 1988, Parrish et al. 1990). Its root system extends up to 3.3 metres and has a greater distribution of root weight at deeper soil depths than other prairie species (Weaver and Darland 1949).

Low N requirements:
Compared to cool season grasses, optimal yields of switchgrass can be obtained with much lower N requirements and response to N may not be observed in the early years of production (Jung et al. 1990). Nitrogen levels in switchgrass biomass are in the order of 0.5%N at full maturity (Balasko et al. 1984) which is approximately 1/2 that of most cool season grass species.

Low P requirements:
On soils with low levels of available P, warm season prairie grasses have higher dry matter yields and have P concentrations approximately 1/2 that of cool season grasses (Morris et al. 1982). An adaptive advantage of C_4 grass species is their use of mychorhizal symbiosis for nutrient uptake, which may help explain the abundance of C_4 plants in prairie soils low in available nutrients (Hetrick et al. 1988).

Low K requirements:
Switchgrass has a lower critical K level than cool season grasses and seldom shows response to K fertilizer (Smith and Greenfield 1979).

Stand longevity:
Adapted switchgrass cultivars harvested for hay have excellent persistence, minimal disease and insect problems and good cold tolerance.

Acid soil tolerance:
Switchgrass will tolerate extremely low pH soils (<5.0) which do not support the growth of cool season grasses or legumes (Jung et al. 1988)

Low harvest costs:
In studies in the northern United States, 1 cut per season maximized biomass yields from switchgrass while most cool season grasses generally require multiple cuts (Wright 1990).

Soil restoring:
Switchgrass is one of the dominant species of the North American prairie that built some of the most productive and rich soils in the western hemisphere.

High ethanol yield:
Switchgrass has a higher combined cellulose and hemi-cellulose content than cool season grasses or legumes (Cherney et al. 1988).

Farmer friendly:
Compared to other warm season grass species, switchgrass is inexpensive to seed and establishes well. It has good seedling vigor, low seed costs, low seeding rates and good herbicide tolerance.

Environmentally friendly:
Switchgrass provides nesting cover and seeds act as a food

Table 1. Promising Warm Season Grasses for Biomass Production and their Native Soil Moisture Class (adapted from White and Madany in Illinois, 1981).

Dry Prairie	Dry-Mesic Prairie	PrairieMesic	Wet-Mesic Prairie	Wet Prairie
Sand Bluestem Little Bluestem Prairie Sandreed	Indian grass Little Bluestem	Big Bluestem Indian grass	Big Bluestem Indian grass Switchgrass Prairie Cordgrass	Prairie Cordgrass

source for birds. The re-establishment of prairie grasses will improve water quality in several ways: annual grain crops responsible for increasing erosion potential will be replaced, ground water nitrate levels (Ramundo et al. 1992) and surface P loading (Sharpley and Smith 1991) will be reduced. Pesticide impacts on wildlife would be reduced because herbicides would be used probably only in the establishment year unlike the annual use of insecticides and herbicides in field crop production.

Other Promising Warm Season Grasses As Biomass Feedstocks

Switchgrass is only one of 1745 C_4 grass species in the world that have been identified as suitable for growing in temperate climates (Stander 1989). In the U.S. alone there are over 300 C_4 grass species (Stander 1989). Probably many of these other native and exotic C_4 perennial grasses hold as much potential as switchgrass. However, if we view "nature as the standard" we should develop mixtures of C_4 grasses using plant materials from North America. The major advantage of switchgrass is that it is relatively inexpensive and easy to establish. However, other common tallgrass prairie species, such as big bluestem (*Andropogon gerardii*) and Indiangrass (*Sorghastrum nutans*), also have high levels of productivity (Gould and Dexter 1986, Stubbendieck and Nielsen 1989, Jung et al. 1990) and deserve significant research attention. The seeding of all three of the major tallgrass prairie species in mixtures rather than using a switchgrass monoculture may play an important role in reducing potential disease and insect problems if large scale biomass production occurs. In the higher rainfall areas of the prairie region, eastern gamagrass (*Tripsacum dactyloides)* has also proven to be very productive (Faix et al. 1980, Kaiser 1989) and may have a role in the implementation of low input, polyculture biomass systems.

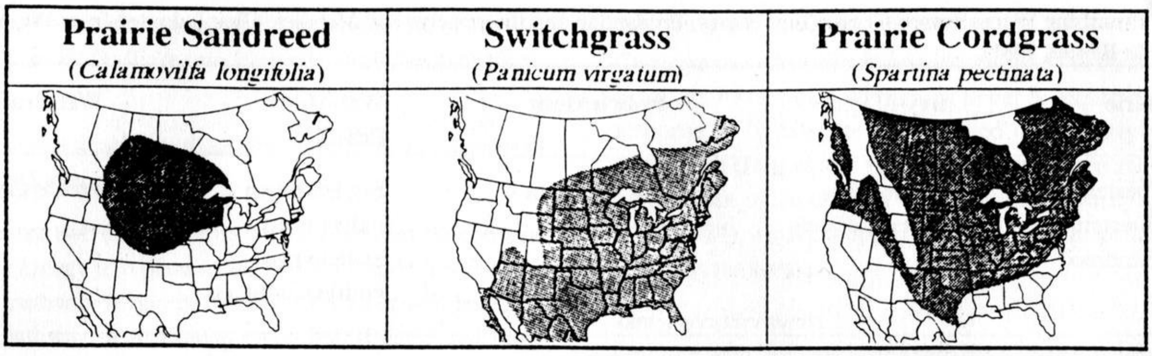
In the native prairie, switchgrass is generally classified as a wet-mesic prairie species (Table 1). Other species are better adapted than switchgrass to the drier or wetter prairie conditions. For example prairie sandreed *(Calamovilfa longifolia)* has outyielded switchgrass in the dry regions of the northern U.S. Great Plains when 25- 35 cm of annual rainfall occurred (USDA 1989). As well, cold resistant, upland switchgrass ecotypes appear to be less adapted to wet prairie conditions than southern lowland switchgrass ecotypes. Using soil moisture as a classification system, we can get a good understanding of how switchgrass, as well as a number of other promising native warm season grasses, are adapted for biomass production (Table 1).

Compared to other warm season grasses, cold tolerance may limit switchgrass productivity. Prairie cordgrass (*Spartina pectinata*) has a more northern native range than switchgrass. Studies have identified a significant amount of chilling tolerance in prairie cordgrass which enables earlier canopy development (Long et al. 1990). However, published yield data is limited on this species. Nitrogen fertilization of native prairie cordgrass stands in Nova Scotia have produced yields of 7.7 t/ha (Nicholson and Langille 1965). Small plot biomass studies in England have produced yields of 8 to 23 t/ha (Long et al. 1990).

Canada's diverse climatic conditions will require a number of C_4 species to be developed as biomass feedstocks. The natural range of prairie sandreed, switchgrass, and prairie cordgrass provide a good idea of how each of the three species has its own unique adaptation. A good starting point for a biomass plant material program in Canada would include these three species as well as big bluestem and Indiangrass which have a similar native range as switchgrass. Prairie ecologists could significantly contribute by collaborating with biomass researchers in developing species and mixtures for various climatic and soil conditions. Prairie ecologists are also uniquely connected to the best gene banks for prairie grasses, the existing prairie remnants. Collecting seed from a large number of productive species and accessions would also contribute to increasing diversity in biomass prairie plantings.

Using Biofuels For CO_2 Abatement

The potential exists for warm season grasses as biofuel feedstocks to be one of the most important energy supply changes for reducing CO_2 emissions. Energy production



Prairie Sandreed (*Calamovilfa longifolia*)

Switchgrass (*Panicum virgatum*)

Prairie Cordgrass (*Spartina pectinata*)

Figure 2. Native range of promising biomass feedstocks.

from warm season grasses changes CO_2 emissions in two ways:

1. it displaces fossil fuels and their high CO_2 emissions;

2. it returns the prairie landscape to a landuse that mimics more closely its original condition, thereby regaining a significant portion of the original carbon lost to the atmosphere through conversion of carbon rich soils to agricultural use.

The production of cellulosic energy contributes a small amount of CO_2 to the atmosphere but only to the extent that fossil fuels are used in their production. The vast majority of the CO_2 released from the conversion of biomass is merely CO_2 that has been sequestered from the atmosphere by plant growth - the carbon contained in the above and below ground biomass. In contrast, large amounts of CO_2 released by fossil fuels are from long term carbon storage. The substitution of cellulosic energy crops for fossil fuels would thus result in a relatively large net reduction of atmospheric carbon dioxide (Turhollow and Perlack 1991).

Table 2. Relative CO_2 emissions per unit of energy for various energy types.

Energy Source	kg C/GJ Energy
Oilsands	30.0
Coal	24.7
Petroleum	22.3
Natural gas	13.8
Switchgrass	1.9

From Hengeveld (1989) and Turhollow and Perlack (1991)

For Canada the greatest potential to reduce CO_2 emissions would come from using switchgrass or other cellulosic biomass crops as a replacement for gasoline derived from the oilsands projects (Table 2). There is no potential for the grain ethanol industry to reduce CO_2 emissions in an equally significant way. U.S. DOE studies indicate that corn ethanol produces 79% of the CO_2 emissions of gasoline (Marland and Turhollow 1990). If included in a 10% blend, this would reduce CO_2 emissions by 2.1%. Any major reduction in CO_2 emissions from fossil fuels will only come from going beyond the 10% ethanol blend. Even if the grain ethanol industry had a significant potential to reduce CO_2 emissions it would be limited by both land base availability and by-product market saturation (making production costs prohibitive). The most significant difference in reducing CO_2 emissions between switchgrass and grain ethanol comes from by-product utilization of the two processes. In the switchgrass ethanol cycle, lignin is the byproduct which can be burned to provide sufficient steam and electricity to complete the entire conversion process. In the grain ethanol cycle, fossil fuel is used for the conversion process and the by-product (distilled grain) is used in an intensive beef feedlot industry. The most recent analysis of the cellulosic ethanol fuel cycle indicates a 91% reduction in CO_2 emissions compared to reformulated gasoline and 4.35 units of output energy are produced for each unit of fossil energy required (Bull et al. 1992).

SUMMARY

Switchgrass is a resource efficient, native, perennial grass which has significant potential as a feedstock for the development of a cellulosic ethanol industry in Canada. It could play a major role in reducing Canadian CO_2 emissions by 1) increasing carbon storage in soil and vegetation compared to present land use and 2) enabling the production of a liquid transportation fuel that will reduce CO_2 emissions by approximately 90% compared to gasoline. The development of this industry could play an important role in helping Canada solve some of its most important problems including job creation, energy security and global warming.

ACKNOWLEDGEMENTS

REAP-Canada's biofuel development work is funded by Agriculture Canada and Natural Resources Canada in Ottawa through the Green Plan's climate change program. We are grateful for the cooperation from the US Department of Energy, US Soil Conservation Service Plant Material Centers and private collectors for donations of plant material and documentation.

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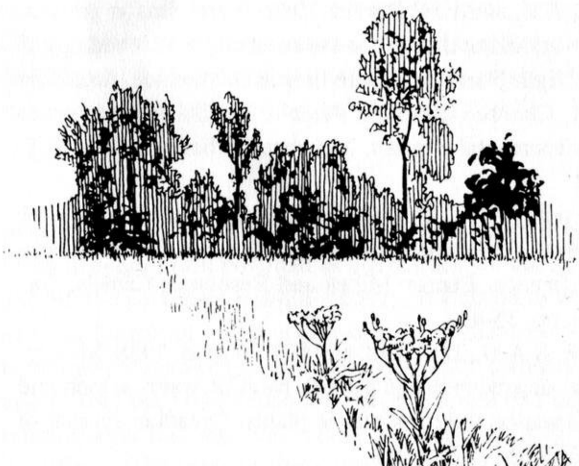

INDEX TO AUTHORS

NORTH AMERICAN PRAIRIE CONFERENCES

The Thirteenth 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 of 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 thirteen 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 of the Proceedings, is included in brackets on the inside back cover.

NORTH AMERICAN PRAIRIE CONFERENCES 1st-13th
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 Centre 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
13th	Lloyd O.W. Burridge, Department of Parks and Recreation, 2450 McDougall Ave., Windsor, ON Canada. 6-9 August 1992.

NORTH AMERICAN PRAIRIE CONFERENCES

Conferences are listed in suggested citation format [with how to order copies and other additional information in brackets].

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SECOND: Zimmerman, James H., Editor. 1972. *Proceedings of the Second Midwest Prairie Conference.* Published by the editor. 242 pages. [For proceedings, make checks for $8.50 (U.S.) payable to "James H. Zimmerman," 2114 Van Hise Ave., Madison, WI 53705.]

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